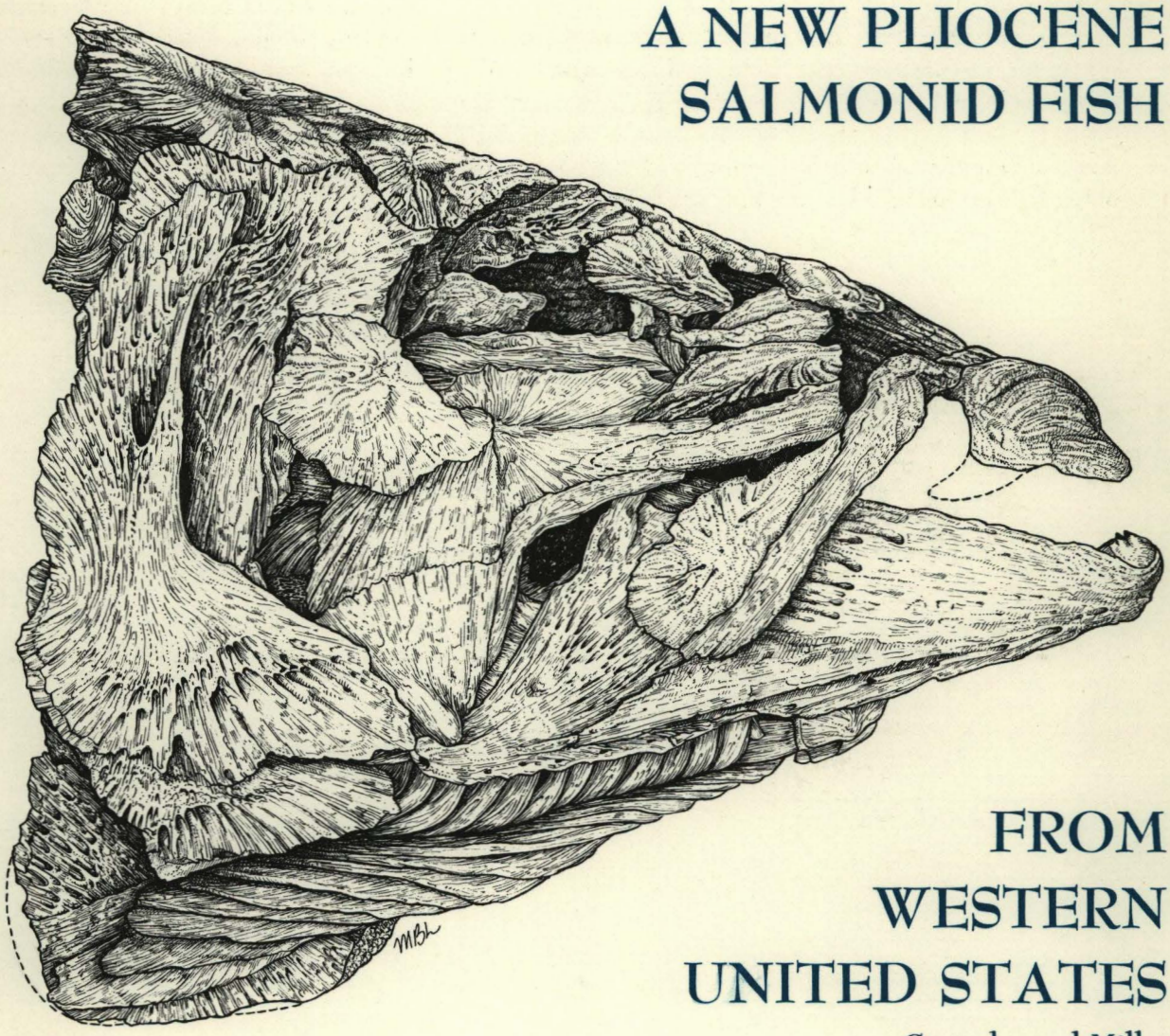
SMILODONICHTHYS RASTROSUS
A NEW PLIOCENE SALMONID FISH



FROM WESTERN UNITED STATES

Cavender and Miller

BULLETIN No. 18
of the
MUSEUM OF
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University of Oregon
Eugene, Oregon
March 1972

The *Bulletin* of the Museum of Natural History of the University of Oregon is published to increase the knowledge and understanding of the natural history of Oregon. Original articles in the fields of Archaeology, Botany, Ethnology, Geology, Paleontology, and Zoology appear irregularly in consecutively numbered issues. Contributions arise primarily from the research programs and collections of the Museum of Natural History and the Oregon State Museum of Anthropology. However, in keeping with the basic purpose of the publication, contributions are not restricted to these sources and are both technical and popular in character.

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LAURENCE R. KITTLEMAN, *Editor*
Museum of Natural History
University of Oregon

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TED M. CAVENDER
Museum of Zoology
Ohio State University

AND

ROBERT RUSH MILLER
Museum of Zoology
The University of Michigan

INTRODUCTION

In western North America, the family Salmonidae is comprised of a diverse number of species (upwards of 30) belonging to seven genera assigned to three subfamilies (Norden, 1961). Though more than half of these species are endemic to the area, an astonishingly few fossil specimens have been discovered which can help document the evolution that has taken place in this group. An exception is the one described in this paper which adds importantly to our understanding of the past life of these fishes.

Materials of this fossil salmonid were collected over a period of fifty years from Pliocene, Pacific-slope localities in California and Oregon. As early as 1917, vertebrae, teeth and skull fragments of an extremely large but unfamiliar type of fish were unearthed, along with mammalian remains, at Pinole, Contra Costa County, California. Only within recent years, however, has it been possible to identify these with certainty as being the remains of an extinct form of salmonid that once was distributed in the coastal regions of the Pacific Northwest, probably much the way that Pacific salmon (*Oncorhynchus*) are today. In 1950 and again in 1964, more complete specimens were discovered of this unusual species from a Pliocene gravel pit in northcentral Oregon. The last find consisted of a large skull which is outstanding for its completeness and detail of preservation. It is a description of this skull that forms the main context of the present paper and which has allowed fruitful comparison to be made with living salmonids.

The name *Smilodonichthys rastrosus* is proposed for this previously undescribed species. Because of its high degree of morphological distinction from other members of the Salmonidae, this species is made the type of a new genus. A number of its osteological features indicate a phyletic relationship closest to *Oncorhynchus*, yet none of the extant species of that genus approaches the fossil in the specialization of its feeding mechanism.

ACKNOWLEDGMENTS

Cooperation from many sources has enabled the completion of this study. We are particularly indebted to J. Arnold Shotwell of the University of Oregon Museum of Natural History, who loaned the material that has provided the basis for distinguishing the new genus. For the loan and gift of other specimens we thank Donald E. Savage of the University of California Museum of Paleontology, C. A. Repenning of the U.S. Geological Survey, and Norman V. Peterson of the Oregon State Department of Geology and Mineral Industries. W. I. Follett provided information leading to study of the Turlock material and Dennis Garber made available the specimens from Turlock Lake. James O. Berkland collected material and provided information on the Worden fossils. H. A.

Vibbert donated material from Gateway, as did Phil F. Brogan. C. H. Ellis and H. A. Demorest of the Washington State Department of Fisheries generously donated a large breeding male Chinook salmon for skeletal preparation. Elizabeth S. Wing loaned a large tarpon skeleton. Richard L. Wilson provided technical help. The carefully executed drawings of the type specimen are the work of Martha B. Lackey, staff artist of The University of Michigan Museum of Zoology, and Louis P. Martonyi took the photograph of the large vertebra. Financial support from the National Science Foundation, GB-4854X and GB-14871 (to R. R. Miller), including publication subsidy, is gratefully acknowledged.

MATERIAL

Institutional abbreviations are: University of Oregon Museum of Natural History (UO), University of California Museum of Paleontology (UCMP), University of Michigan Museum of Paleontology (UMMP), and University of Michigan Museum of Zoology (UMMZ).

The following material is all from Oregon.

Holotype, UO 26799, Gateway Locality, collected by Mrs. George Iiames and Scott McKain, summer 1964: skull with jaws and anterior gill arches in articulated condition; opercles and subopercles missing (see Figs. 3-6, 10).

Paratype, UO F3335, Gateway Locality, collected by J. A. Shotwell and first discovered by Miss Ann Brownhill about 1950; associated parts from a single individual of very large size (somewhat larger than holotype) are listed as follows: badly crushed neurocranium showing posterior portion of parasphenoid, basioccipital, both exoccipitals and prootics; flattened on top of these bones are portions of the frontal, parietal, epiotic and pterotic (all of the left side), plus part of the supraoccipital; complete right and left mandibles and premaxillae, to each of which is firmly attached an extremely large breeding tooth (Fig. 9) with ossified base; left maxilla; right and left quadrate; right hyomandibular; right ceratohyal; portions of three branchiostegal rays; part of the right preopercle; posterior part of the right cleithrum; complete right posttemporal and incomplete left posttemporal; miscellaneous fragments including parts of opercle, pectoral fin, basihyal plate, neural and hemal spines, branchial arches; approximately 40 vertebrae, both from the caudal and precaudal series; left epihyal; left interopercle; left lacrimal; right supraorbital.

UMMP V58061, about 20 vertebrae probably belonging to the paratype, Gateway Locality, R. R. Miller and field party, 1961.

UMMP V58062, five vertebrae probably belonging to the paratype, Gateway Locality, P. F. Brogan, Bend, Oregon, about 1950.

UMMP V58063, left hyomandibular possibly from the paratype, Gateway Locality, H. A. Vibbert, Madras, Oregon.

UMMP V58064, anterior portion of right dentary (Fig. 13) from a juvenile, Worden Locality, Norman V. Peterson, 1968.

Listed below is the material from California.

UCMP 65630, broken premaxillary tooth, Pinole Locality, C. Stock, 1917.

UCMP 22560, water-worn precaudal centrum, Pinole Locality, C. Stock, 1917.

UCMP 34566, central part of left preopercle and seven vertebral centra (some broken or crushed), Pinole Locality, WPA field party, 1938.

UCMP 37584, left premaxilla and tooth, Pinole Locality, WPA field party, 1940.

UCMP 65629, fragments of one vertebral centrum, Pinole Locality, C. Hotton, 1960.

UCMP 58570, incomplete, precaudal vertebral centrum, Pinole Locality, D. Savage and field party, 1961.

UCMP 61554, water-worn premaxillary tooth, Pinole Locality, Preston Ritter, 1962.

UCMP 61039, broken premaxillary tooth, Pinole Locality, Jean Firby, 1962.

UCMP 64100, parts of three vertebral centra, Pinole Locality.

UCMP 61550, right premaxillary tooth with tip missing, Pinole Locality, Melvin Washington.

UCMP 48657, part of vertical limb of left preopercle and part of sensory canal bone, Turlock Locality.

UCMP 44668, right frontal and 2 vertebral centra, Turlock Locality, 1954.

The following California material was collected at the Turlock Locality by Dennis Garber of Modesto, California, from 1957 to about 1964.

UCMP 93170, anterior end of right dentary.

UCMP 93171, articular fossa of right opercle.

UCMP 93172, portion of left frontal.

UCMP 93173-75, three large fragments interpreted as parts of the vertical limbs of preopercles.

UCMP 93176, fragmentary right premaxilla with osseous base of large tooth, in 2 pieces.

UCMP 93177, water-worn left premaxilla with tooth base.

UCMP 93178, right premaxilla with tooth base.

UCMP 93179, complete right premaxilla and tooth.

UCMP 93180, left premaxilla with complete tooth, most of enamel present, anterior portion of premaxilla broken off.

UCMP 93181-83, three left premaxillae with teeth, enamel portions mostly broken off, osseous bases complete.

UCMP 93184, complete right premaxilla and tooth, enamel portion worn.

UCMP 93185, eight vertebral centra (4 complete), largest 40 mm diameter, smallest 30 mm.

UCMP 93186, four bone fragments.

UCMP 93187, one tooth fragment.

LOCATION AND AGE

Fossils referable to *Smilodonichthys* have been found at four main localities, two in California and two in Oregon, plus additional minor sites along the Columbia River of Oregon. In two of the four localities, mammalian fossils have been recovered along with the fish remains and have supplied the valuable mammalian-age determinations.

A. Gateway Locality—UO loc 2250. Collected from a coarse boulder and gravel facies in the "Torrential Beds" (Shotwell's informal name) of the Madras Formation, near the town of Gateway, Jefferson County, Oregon; elev. ca. 2,250 ft. (Figs. 1-2). This unit consists of a mass of boulders, tree fragments, chunks of sediment from the underlying formation of Barstovian (Late Miocene) age, and numerous small sand lenses. Large salmonid vertebrae and, less frequently, teeth have been found along the bottom of these lenses.

The age of the "Torrential" unit is not definitely established. It contains reworked Barstovian vertebrates. According to Shotwell (pers. comm.), the age can be no older than Barstovian nor younger than Hemphillian (Middle Pliocene). There is a strong possibility that the Torrential Unit is of Hemphillian age. *Smilodonichthys* vertebrae have been recovered from Early Pliocene to Late Middle Pliocene deposits along the Columbia River in the vicinity of Arlington, Oregon, and twenty miles to the east.

B. Worden Locality—Abandoned railroad cut near Worden, Klamath County, Oregon, located in the Klamath Falls Quadrangle, collected by Norman Peterson, Oregon State Department of Geology and Mineral Industries, April 15, 1968. This locality consists of a 20-foot deep exposure of tuffaceous sandstone dipping 10 degrees to the northeast which is truncated at the east and west edges of the railroad cut by basaltic intrusions. The sandstone in places is cross-bedded and moderately well cemented. It may belong to the Yonna Formation which is Pliocene (Newcomb, 1958). Bones, including those of land mammals, found at the site were disarticulated and haphazardly assembled during deposition of the sand. Other fish remains that are associated with the salmonids belong to the families Cyprinidae and Catostomidae.

C. Pinole Locality—Pinole Tuff at Pinole, Contra Costa County, California, about 17 miles north of Oakland; UC loc V2572, V3425 and V3837. The locality has yielded a frag-

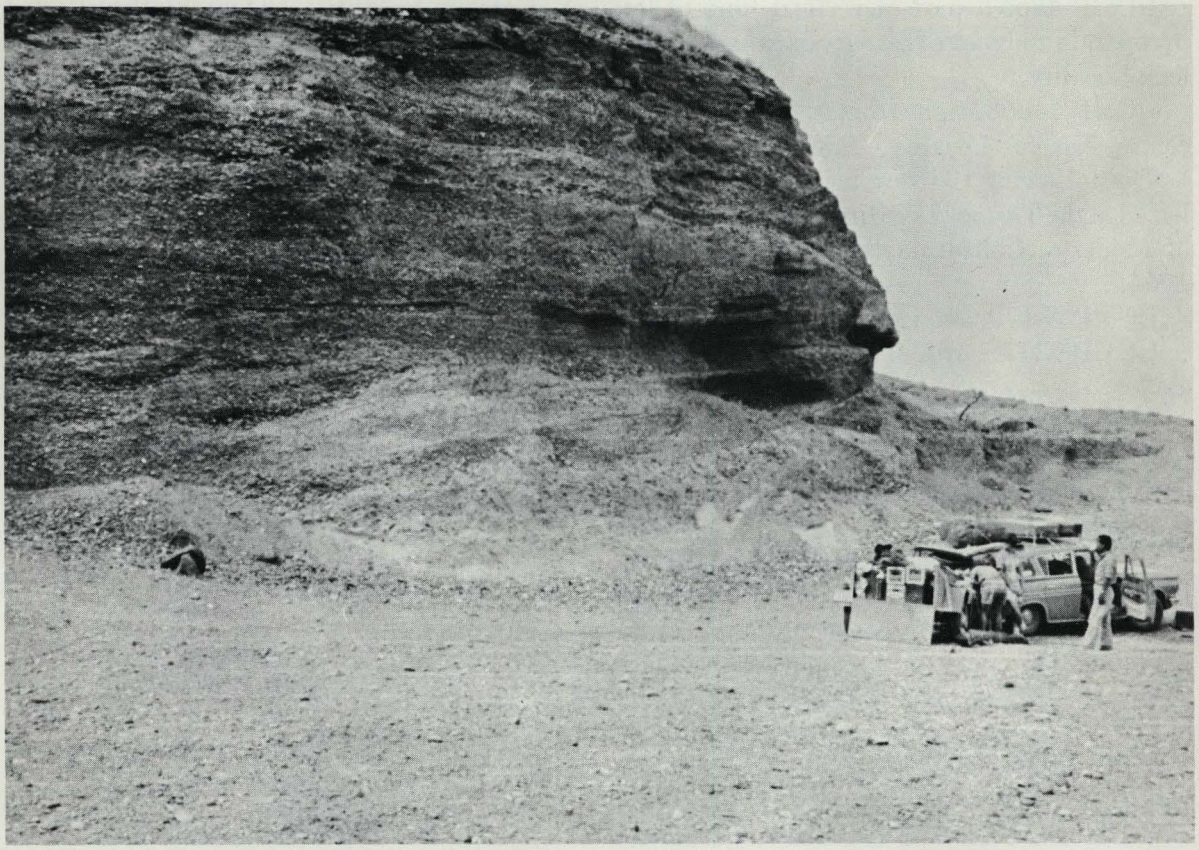


Figure 1. *Gateway Locality, showing exposure of the "Torrential beds" of the Madras Formation, at gravel pit near Gateway, Oregon, 1961.*

mentary mammalian fauna (Stirton, 1939). There is a potassium argon date of 5.2 million years (Evernden *et al.*, 1964) for the Pinole Tuff.

D. Turlock Locality—This locality consists of exposures of the Mehrten Formation which outcrop at the edge of Turlock Lake, Stanislaus County, California, 22 miles east of Modesto. UCMP loc V5405 lies in the NW ¼ of SE ¼ of Sec. 8, T4S, R13E, Turlock Lake Quadrangle (USGS 1953). This site has also yielded a fragmentary land mammalian fauna.

The Turlock Lake and Pinole Localities are chronologically very closely related in terms of the land-mammal fossils which, according to D. E. Savage (pers. comm.), are judged to be a Late Hemphillian (Late Middle Pliocene) river-border fauna.

SYSTEMATICS

Order Salmoniformes
family Salmonidae
SMILODONICHTHYS, new genus

TYPE SPECIES: *Smilodonichthys rastrosus*, new species

(Figs. 3-13)

DIAGNOSIS: Distinguished from all known salmonid species by its numerous gill rakers, over 100 on the first branchial arch in the adult. Jaws and palate without feeding teeth; lower jaw very deep at coronoid process (greatest depth 3 times in length), without tooth-bearing region except an abbreviated shelf adjacent to the symphysis; maxilla toothless, apparently no teeth on palate and tongue; gill rakers and basibranchials toothless. Teeth of breeding in-

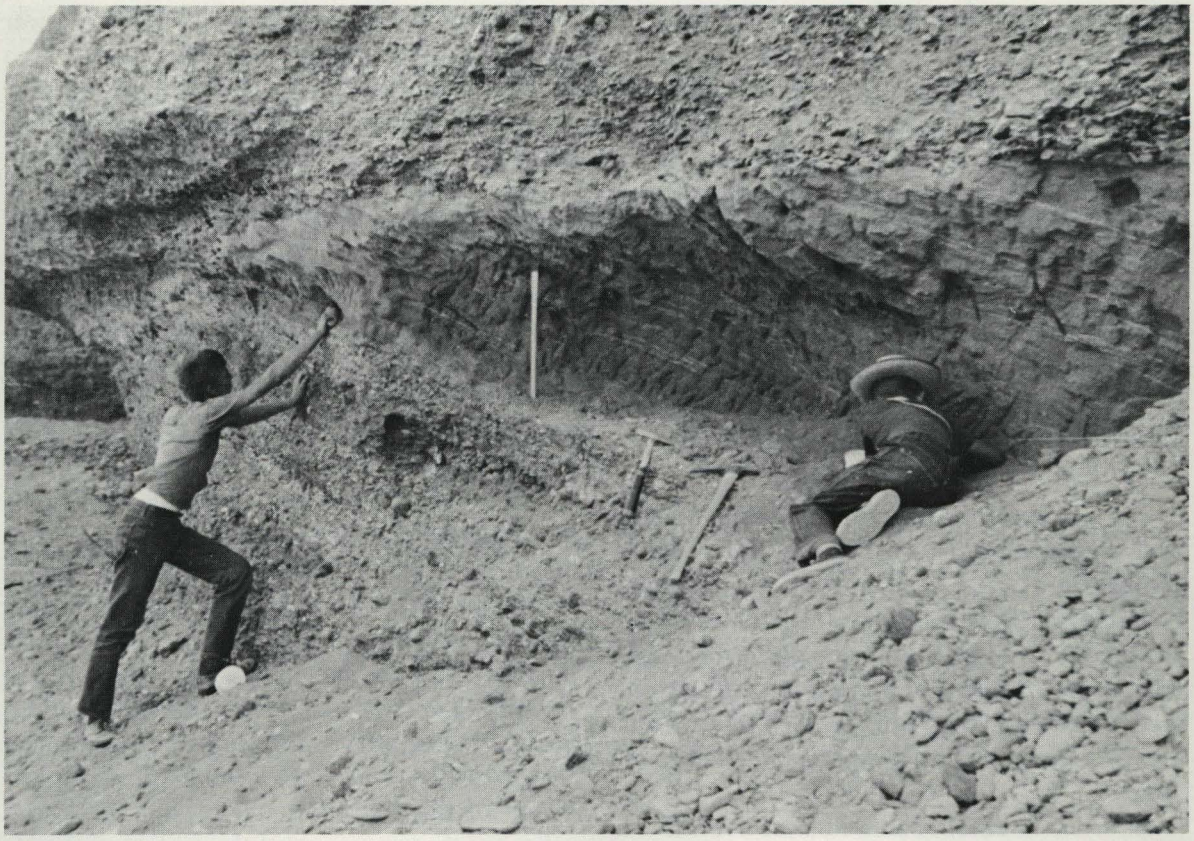


Figure 2. *Detail of the horizon (sand lens being worked) which yielded the paratype of* Smilodonichthys rastrosus *at Gateway, 1961.*

dividuals consist of one massive tooth on each premaxilla and much smaller teeth on the dentaries, usually one at each side of the mandibular symphysis. Supramaxilla exceptionally large, attaining 80% of length of oral border of maxilla. Posterior (basicranial) part of parasphenoid strongly compressed in the form of a keel. Posttemporal fossa very shallow and of small area; dermal part of pterotic lateral to posttemporal fossa, relatively wide. Interopercle with pronounced dorsal extension. Vomer diamond-shaped, with no tooth-bearing platform on shaft. Urohyal 4/5 as long as lower jaw. Ornamentation of vertebral centra consisting of many fine, elevated ridges running longitudinally.

MEASUREMENTS: The length of the neurocranium from the anterior tip of the supraethmoid to the posterior end of the supraoccipital measures 307 mm. Ventrally the length measured from the anterior tip of the vomer to the posterior end of the basioccipital is 316 mm. Interorbital width about 157 mm; width at the attachment of the nasals 103 mm, and width at the frontal-supraethmoid junction 77 mm. Width between the sphenotic processes is 170 mm, between the pterotics 166 mm. Greatest posterior width of parasphenoid (at the ascending wings) 89 mm, greatest anterior width 67 mm. Depth of the neurocranium is markedly distorted due to the dorsoventral compression and loss of cartilage during fossilization.

In the branchiocranium, the distance on the right side between the anterior end of the mandible and the posterior border of the preopercle is 385 mm. The vertical distance on the right side from the horizontal line formed by the

ventral border of the interopercle to the dorsal border of the hyomandibular is 240 mm.

The right mandible measures 264 mm in length and 87 mm in depth at the coronoid process. The maxilla, with supramaxilla in place, measures 150 mm in length and 47 mm in greatest depth. The supramaxilla is 104 mm in length and 32 mm in greatest depth.

The right preopercle, with ventral border broken, measures about 200 mm in height.

The right premaxilla is 76 mm long; the osseous base of the single large tooth on the right premaxilla is 35 mm in greatest width and about 50 mm in greatest length.

The basioccipital condyle is about 45 mm wide (somewhat distorted due to dorsoventral compression). A precaudal centrum, taken from the paratype, is 35 mm in greatest diameter and 25.5 mm in anterior-posterior length (the largest vertebra of *Smilodonichthys* examined, UCMP 44668, from Turlock Lake, measures 48 mm greatest diameter and 28.5 mm long).

In order to obtain some idea of overall size of the holotype, we have made corresponding measurements on skulls of two *Oncorhynchus tshawytscha*: UMMZ 178987-S, 985 mm S.L., 39½ lbs., male, and UMMZ 186299-S, 845 mm S.L., 28½ lbs., female. In that species the length of the opercle averages about 20 percent of head length. Using this proportion, the head length of the fossil (opercle missing) is estimated to be 462 mm. Through a linear progression taken from the proportion of head length to standard length, the fossil is calculated to have had a standard length of 1900 mm.

CRANIAL MUSCULATURE: A number of the individual characteristics of the skull bones in *Smilodonichthys* are associated with places of muscle and ligamentous attachment. In order to interpret more accurately some of these structures, comparisons are made between the fossil and a living salmonid, *Oncorhynchus kisutch*, in the areas of the lower jaw and suspensorium.

The adductor mandibulae is divided by an aponeurosis into an anterior (mandibular) part housed in the meckelian fossa of the lower jaw and a posterior part covering a large area of the cheek between the preopercle and eye (Greene and Greene, 1914). In addition, the posterior part is split into three poorly defined divisions (A_1, A_2, and A_3 of Allis, 1897) which are best delineated where the muscle takes its origin. The longest division, A_1, has its origin dorsally on the well developed adductor ridge of the hyomandibular. It runs downward behind the eye to the aponeurosis situated at the coronoid margin of the articular. The second and largest division, A_2, originates principally on the anterior edge of the preopercle and adductor ridge but fibers are also attached to the quadrate and symplectic. The A_3 division runs underneath and obliquely to the first two. It originates on the lateral face of the ascending wing of the metapterygoid. The mandibular portion of the adductor muscle inserts on the strong ledge that runs along the ventromesial part of the dentary. This ledge is a prominent feature on the dentary of *Smilodonichthys*. The extent of the meckelian fossa which provides room for the expansion of the adductor muscle during contraction is greater in *Smilodonichthys* than in *Oncorhynchus*. Also, in the former, the adductor ridge presumably serving as the area of origin for the A_1 and A_2 divisions is more pronounced and may exclude part of the upper limb of the preopercle as a place of muscle attachment.

Two muscles that operate the suspensorium are the adductor and levator arcus palatini. The former originates on the lateral face of the ascending process of the parasphenoid and on the anterior rim of the prootic. It inserts on the posteromesial extension of the endopterygoid. Both of these areas are developed to a greater degree in *Smilodonichthys* than in *Oncorhynchus*. A ridge transversely crosses the endopterygoid beneath the orbit of *Smilodonichthys*, possibly marking the anterior limit of insertion of the adductor arcus palatini. The levator has two major divisions. The anterior (outer) division inserts on the mesial side of the ascending wing of the metapterygoid. The innermost posterior division inserts on the lateral surface of

the hyomandibular head. The levator origin is on the sphenotic process and the pterotic. The opposite (mesial) side of the hyomandibular head forms a large area for insertion of the hyomandibulae muscle that takes its origin principally from the prootic. In *Oncorhynchus kisutch*, this muscle is subdivided into an anterior and posterior part at its insertion. In both *Smilodonichthys* and *Oncorhynchus*, the head of the hyomandiublar is exceptionally broad.

On the back of the braincase at each side of the foramen magnum are shallow fossae for insertion of anterior trunk musculature. These muscles pass forward between the vertebral column and pectoral girdle to their place of attachment (Gosline, 1969). The posterior processes of the pterotics lie lateral to them and apparently form a support for the pectoral girdle at the point where the posttemporal is expanded ventrally. They also serve as a place of origin for part of the levator operculi. The fossae at each side of the foramen magnum appear to be in line with the row of anterior epineural ribs. Even when taking into consideration significant depression of the braincase during preservation, the depth of the rear wall of the braincase is greater in *Oncorhynchus* than it is in *Smilodonichthys*. The former also has much larger posttemporal fossae for insertion of the more dorsal portions of the anterior trunk muscles. The difference pointed out in rear skull proportions and body muscle attachment may indicate that *Oncorhynchus* has a greater body depth than was present in *Smilodonichthys*.

ETYMOLOGY: Named *Smilodonichthys*, from the fossil genus of sabre-toothed cat, in reference to the pair of large teeth at the anterior end of the upper jaw, and *rastrosus*, from the Latin word for raker, in reference to the numerous gill rakers.

DESCRIPTION

NEUROCRANIUM: The neurocranium was disarticulated from the rest of the skull to enable careful study and illustration. Preservation was virtually complete, but some lateral distortion and depression (especially in the orbitosphenoid-pterosphenoid region) occurred in fossilization.

Cranial Roof.—The most striking characteristics of the cranial roof (Fig. 3) are: (1) the overall size and elongate shape; (2) the heavily ossified construction of the component bones, especially the frontals; (3) the completeness of the bone-roofing posteriorly and the shallow posttemporal fossae; (4) the supraoccipital separating the parietals; (5) the frontals not entirely meeting over part of their midline; and (6) the triangular-shaped supraethmoid.

In area covered, the *frontals* are the major bones of the cranial roof. An incomplete right frontal, UCMP 44668, showing the central and lateral portions of the bone where it articulates with the sphenotic, is thick and massive in appearance. It indicates that the frontals were very strong where they form a low arch between the sphenotics. The oblique ridge on the lower frontal surface that unites with the sphenotic is exceptionally well developed. It lies under the heaviest part of the frontal. As in Recent *Oncorhynchus*, the fit between the frontal and sphenotic is so close that the line of junction is barely perceptible. Mesially, the frontals are very thin. They meet in the midline where they overlap the supraoccipital, near the middle of the cranium between the sphenotics, and probably also at their anterior ends where they contact the supraethmoid. Two large spaces in the midline, one ahead and one behind the zone of frontal contact in the area between the sphenotics, indicate regions occupied by cartilage. A similar separation of the frontals by cartilage occurs in Recent *Oncorhynchus*. The frontals are very long bones with most of the trabeculae running longitudinally. The trabeculae can be traced by ridges on the surface of the bone. Structurally, the frontals form strong bracing beams between the pterotics at the rear of the cranial roof and the supraethmoid in front.

The pattern of the surface ridges in the central portion of the frontals, where they bridge between the sphenotics, indicates that they meet compressional stresses from the sides probably set up by the suspensorium.

The anterior part of the cranial roof tapers to a point through the triangular shape of the median *supraethmoid*. The posterior extensions of this bone overlap the frontals on each side. The posterior limits of the supraethmoid are not clear. However, there may be a notch in the posterior border. In outline, the supraethmoid is similar to that of *Oncorhynchus kisutch* and *O. masou* (Vladykov, 1962: Figs. 28-29). It differs in its sturdier construction. Norden (1961) found that within the salmonines, the supraethmoid has the greatest taxonomic signficance of all the dorsal roofing bones. *Nasals* are present, fastened to the lateral edges of the frontals just behind the supraethmoid.

One of the obvious differences in the cranial roof between the fossil and *Oncorhynchus* is the very limited development of the posttemporal fossae. There may be some distortion, due to partial flattening of the neurocranium, but even accounting for this, the fossae are shallow and short. The floor of the fossa, formed by the frontal, epiotic and pterotic, is apparently a continuous covering of bone. There is no cartilaginous interspace as in Recent salmonines.

Ventral Bones of the Neurocranium.—When viewed from below, the general appearance of the neurocranium (Fig. 4) again is that of an *Oncorhynchus*. The *parasphenoid* is very broad anteriorly. With the vomer attached, it dominates the whole lower surface. In addition to its anterior breadth and total length, this bone is distinctive in the form of its posterior extension and in the length of its ascending wings. The posterior extension forms the bottom of the eye-muscle canal or posterior myodome and meets the basioccipital and prootics. Instead of being broadly rounded, allowing the myodome to have a substantial opening to the posterior as in *Oncorhynchus*, it is laterally compressed to a point where the myodome is a narrow channel. Thus the parasphenoid is markedly keel-shaped. The closest comparison among the Salmonidae can be found in *Coregonus*, in which the posterior part of the parasphenoid is somewhat keel-shaped, with large lateral surfaces. However, this part is not much compressed and the myodome has a wide posterior opening.

At the anterior end of the ossified braincase, the ascending wings of the parasphenoid extend high up on the anterior margins of the prootics and may have reached as far as the sphenotics. Each ascending wing has a long free anterior edge that curves to a junction with the main longitudinal part of the parasphenoid. At this point of junction, the parasphenoid is quite narrow but very thick. The thickened area and the ascending wings present an exceptionally long and sturdy place of origin for the adductor arcus palatini muscles already mentioned in *Oncorhynchus*. Just posterior and mesial to the ascending wings, a pair of foramina are visible that penetrate the parasphenoid directly below the anteroventral corner of the prootic. They are the openings for the internal carotid arteries that are positioned as in Recent *Oncorhynchus*. Unlike the latter, however, there appear to be no openings for passage of the efferent pseudobranchial arteries within the parasphenoid itself.

Anterior to the ascending wings, the thickening of the parasphenoid extends forward along its lateral edges as the bone gradually widens. The parasphenoid reaches its greatest width just ahead of the lateral ethmoids. The broad anterior portion of the parasphenoid is matched by a broad posterior half of the *vomer* which overlaps it. The latter possesses a distinctive shape when compared with other salmonines. It looks like an elongated diamond. At the tapered anterior end, the lateral edges parallel those of the supraethmoid above. Also, at the anterior end, the vomer is thickened, but there is no evidence of a pronounced constriction that sets it off from the posterior part. It is possible that the edges may have extended farther laterally forming a "head," since there is some evidence of breakage. One striking feature of the vomer is the absence of teeth or of any kind of tooth-bearing platform.

There are no other ossifications visible in the ethmoid region than those described. It is concluded that the area between the supraethmoid and vomer must have been occupied by a large ethmoid cartilage, as in *Oncorhynchus* and other salmonines.

The bones of the otic region are similar to those of *Oncorhynchus* in their shape and relationships to each other. One apparent difference concerns the lateral process of the *sphenotic* which projects directly outward instead of curving backward to form a well defined fossa. Also, the anterior border of the *prootic* is in contact for most of its length with the ascending wing of the parasphenoid.

Both posterior processes of the *pterotics* are broken off in the holotype. These are well developed in *Oncorhynchus* and other salmonines but less pronounced in coregonines. There is a long, well-defined groove on the ventral surface of each pterotic which extends obliquely forward along the zone of contact between the prootic and sphenotic. This groove seats the head of the hyomandibular. The *intercalars* are present at the posterior corners of the braincase. They possess long projections that extend anteriorly to unite with, and partly extend onto, the prootics. At the posterior end of the basicranium the *basioccipital condyle* is formed by the fusion of the first vertebral centrum (proatlas) with the basioccipital in both the holotype and paratype. This structure forms the entire circular facet for articulation with the vertebral column, excluding the exoccipitals. The lines of contact between the exoccipitals and the proatlas are visible in these two specimens.

At the anterior end of the braincase a pair of badly crushed, highly cavernous ossifications are present that represent the *pterosphenoids*. Neither the *orbitosphenoid* nor *basisphenoid* was preserved.

BRANCHIOCRANIUM: Except for the absence of the gill covers, the external bones of the branchiocranium (Figs. 5-6) are nicely displayed on the holotype and needed very little preparation. Internally, however, the orobranchial cavity was completely filled with coarse sand and gravel which had to be removed to expose the gill arches and associated elements.

The branchiocranium possesses a complex of distinctive, yet interrelated, characters that nearly all appear to be associated with the un-

ABBREVIATIONS USED ON THE ILLUSTRATIONS

Ao = antorbital
A R = adductor ridge of hyomandibular
Art = articular
Bh = basihyal
Boc = basioccipital
Br = branchiostegals
L Br = left branchiostegals
R Br = right branchiostegals
C I = cartilage interspace
L DA 1, 2, 3 = left dorsal limb of gill arch
R DA 1, 2, 3 = right dorsal limb of gill arch
De = dentary
L De = left dentary
R De = right dentary
De T = dentary teeth
Dsph = dermosphenotic
Ect = ectopterygoid
End = endopterygoid
Eoc = exoccipital
Epo = epiotic
Fr = frontal
f ic = foramen for internal carotid artery
f j = jugular foramen
f VII = foramen for 7th cranial nerve
f X = foramen for 10th cranial nerve
D Hh = dorsal hypohyal
V Hh = ventral hypohyal
Hm = hyomandibular
L Hm = left hyomandibular
R Hm = right hyomandibular
Int = intercalar
Io 2-6 = infraorbitals 2-6
L Iop = left interopercle
R Iop = right interopercle
La = lacrimal
L E = lateral ethmoid
M Ca = mandibular canal
Met = metapterygoid
Mx = maxilla
L Mx = left maxilla
R Mx = right maxilla
Na = nasal
OBT = osseous base of tooth
Op = opercle
Pa = parietal
Pal = palatine
Pmx = premaxilla
Pmx T = premaxillary tooth
Pop = preopercle
Pra = proatlas (fused first centrum)
Pro = prootic
Ps = parasphenoid
Pt f = posttemporal fossa
Pto = pterotic
Pts = pterosphenoid
Qu = quadrate
Se = supraethmoid
Smx = supramaxilla
So = supraorbital
Soc = supraoccipital
So Ca = supraorbital canal
Sph = sphenotic
Sop = subopercle
Spop = suprapreopercle
Sy = symplectic
Uh = urohyal
L VA 1, 2, 3 = left ventral limb of gill arch
R VA 1, 2, 3 = right ventral limb of gill arch
Vo = vomer

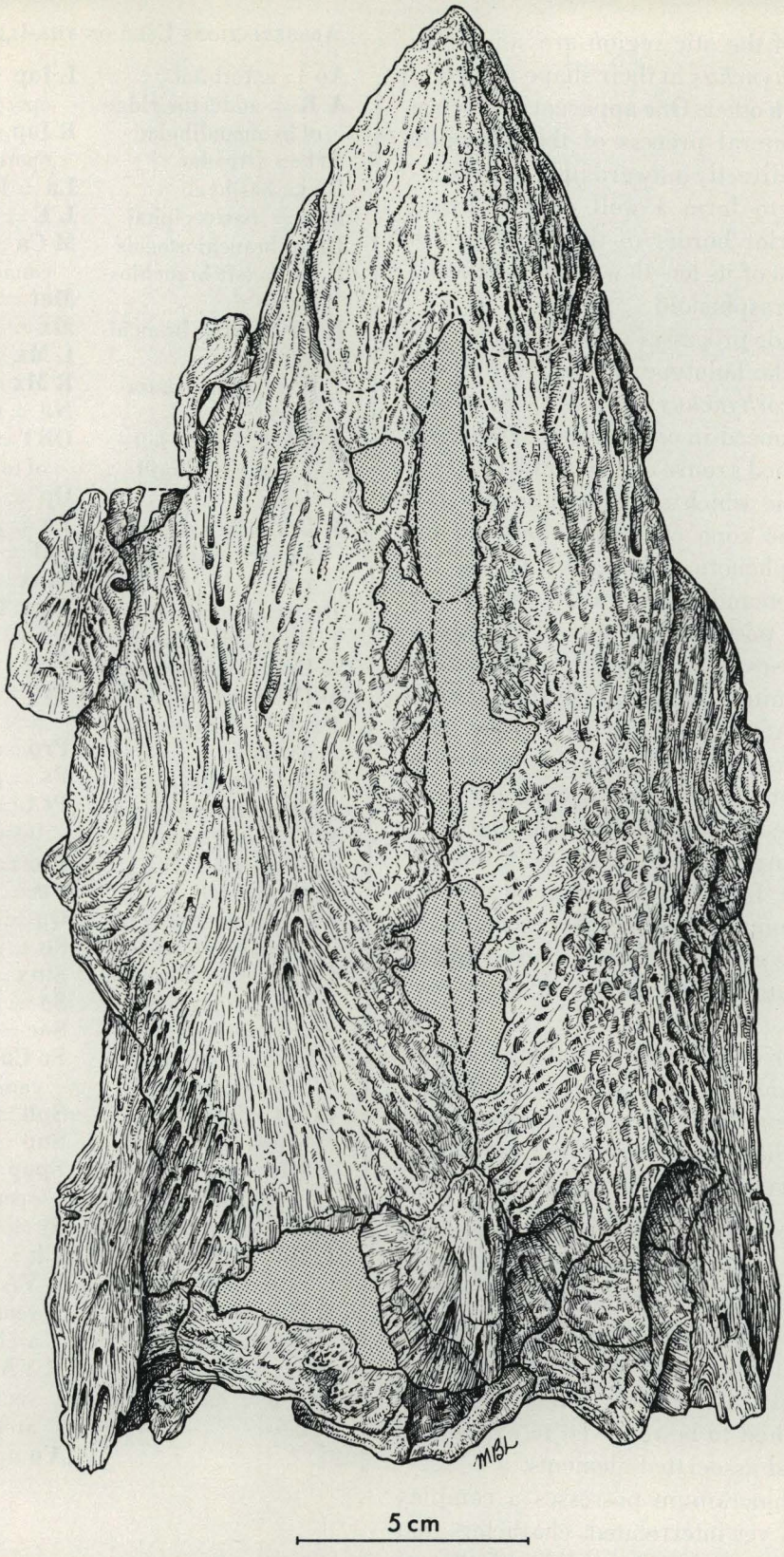
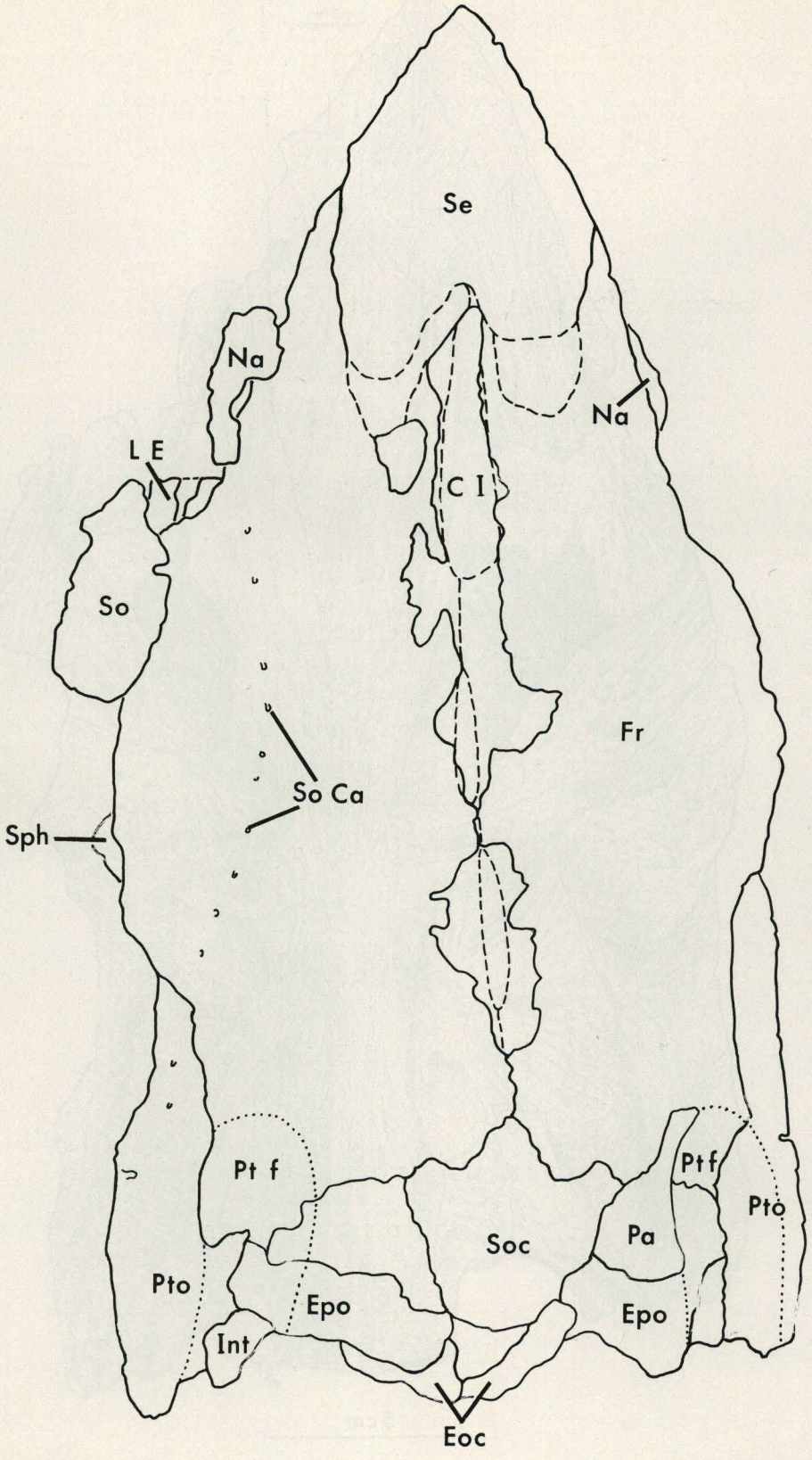


Figure 3. *Cranial roof of holotype of* Smilodonichthys rastrosus. *Abbreviations are given on the preceding page.*


Se
Na
Na
L E
C I
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Fr
So Ca
Sph
Pt f
Pt f
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Soc
Pa
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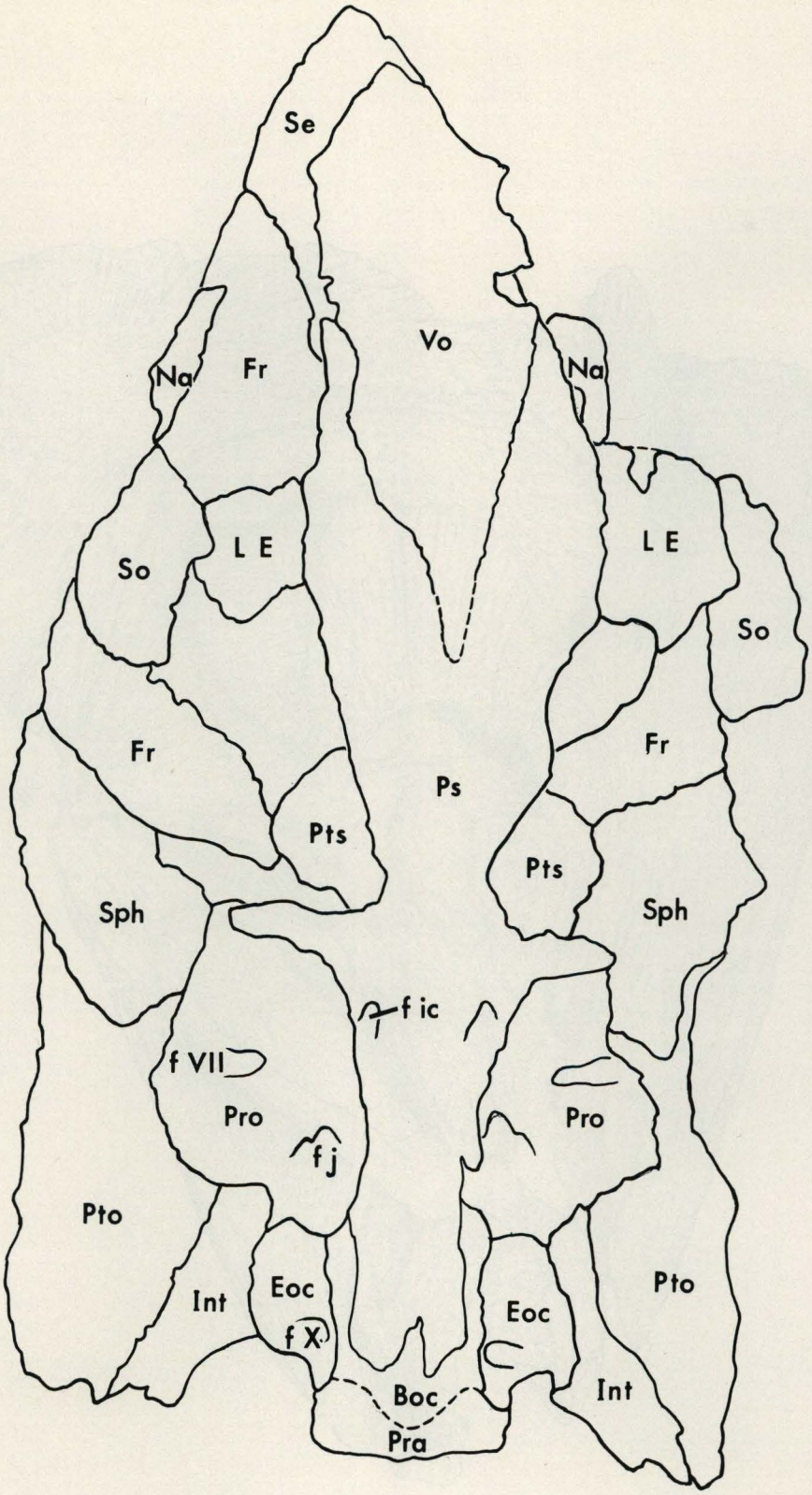
Int
Eoc

Figure 4. *Ventral view of neurocranium of holotype. Abbreviations are given on the page preceding Figure 3.*


Se
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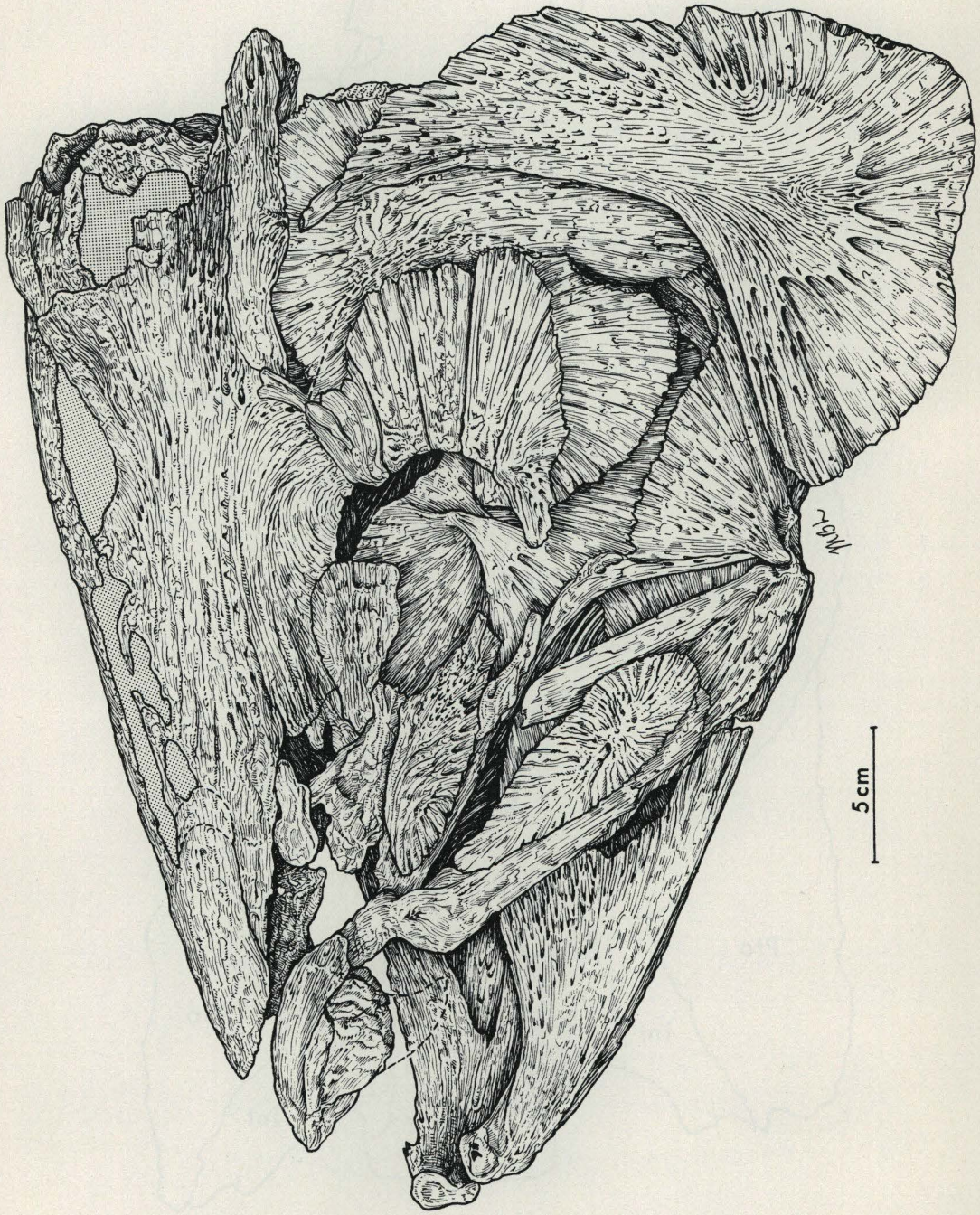
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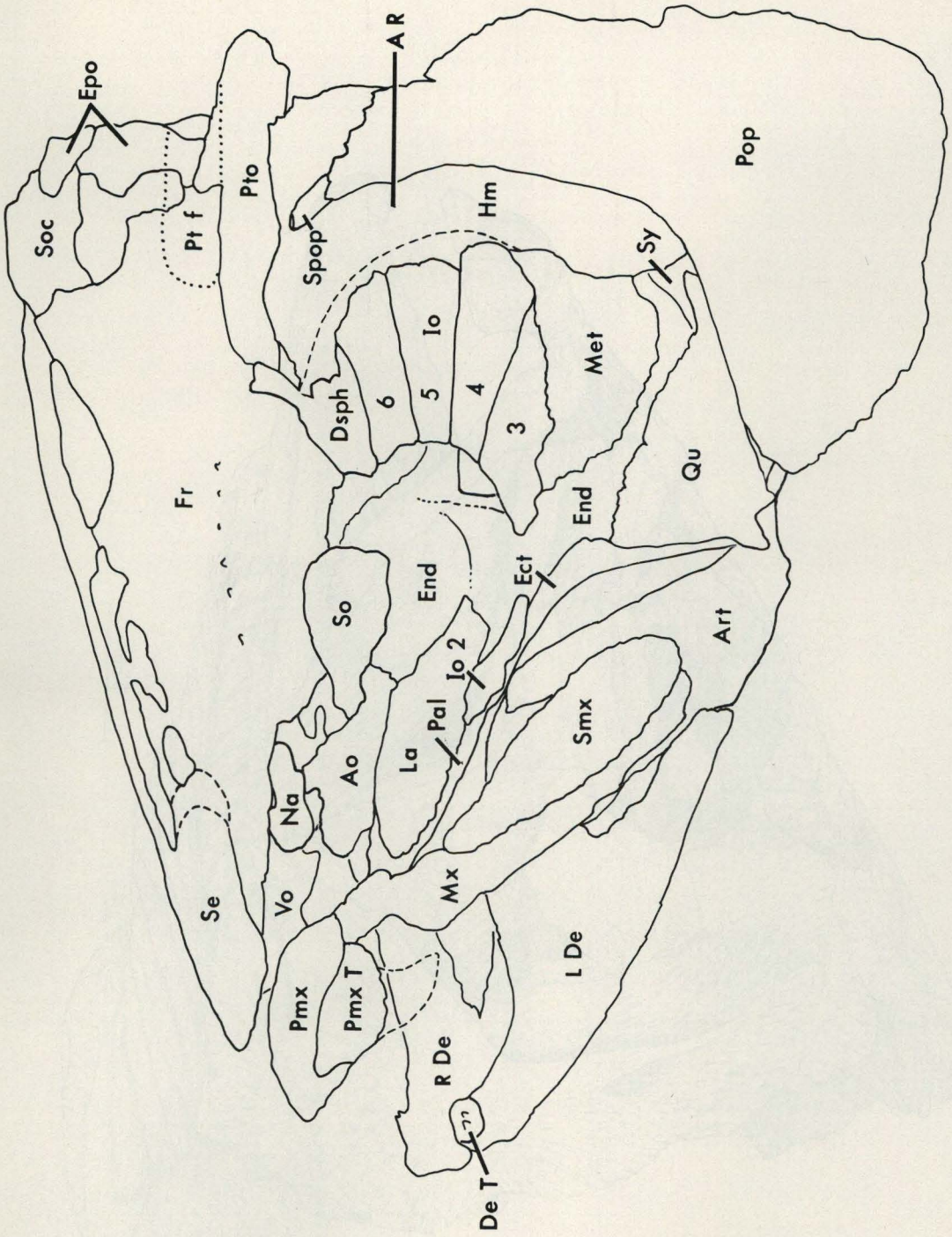
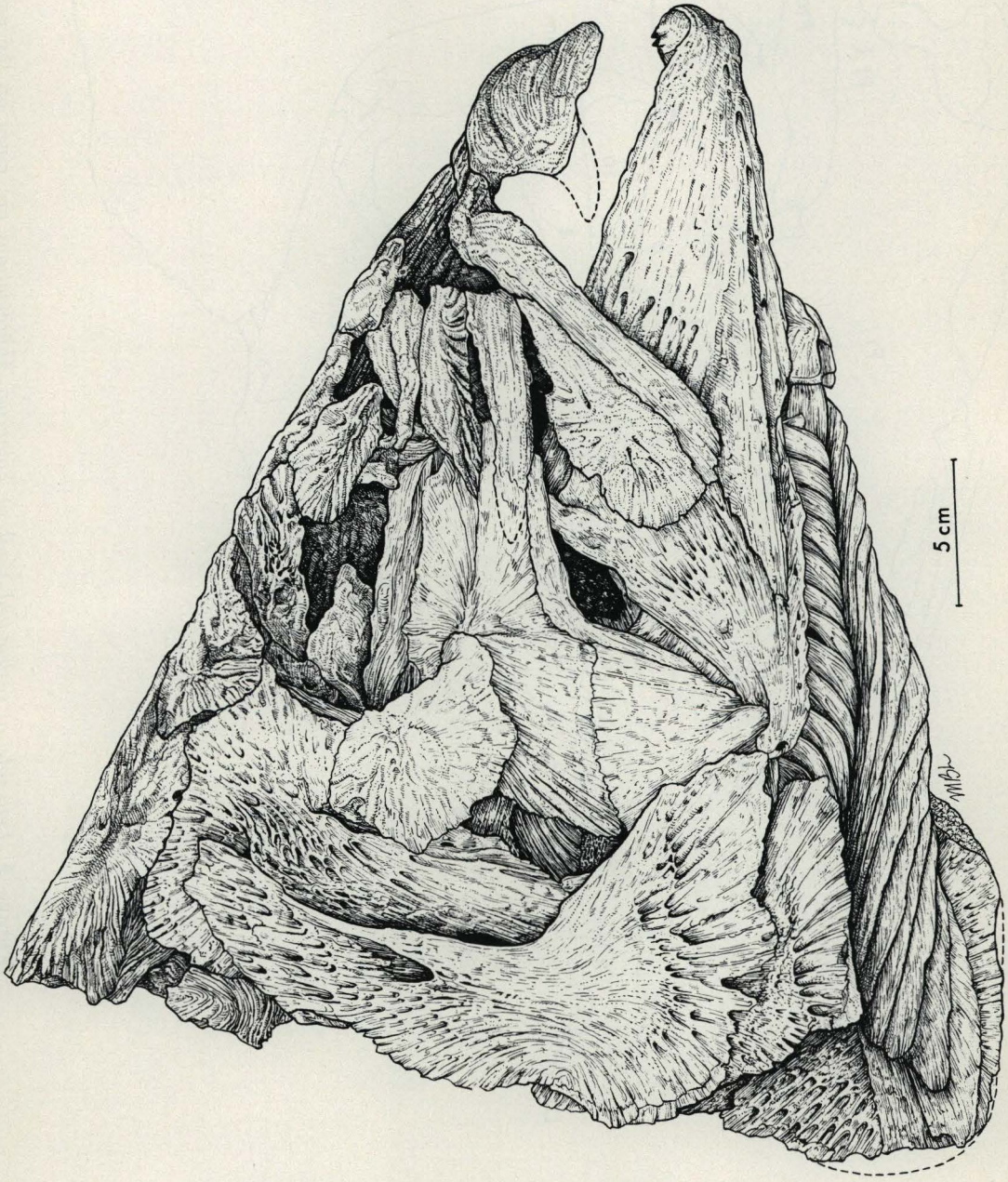


Figure 5. *Left side of articulated skull of holotype. Abbreviations are given on the page preceding Figure 3.*


5 cm

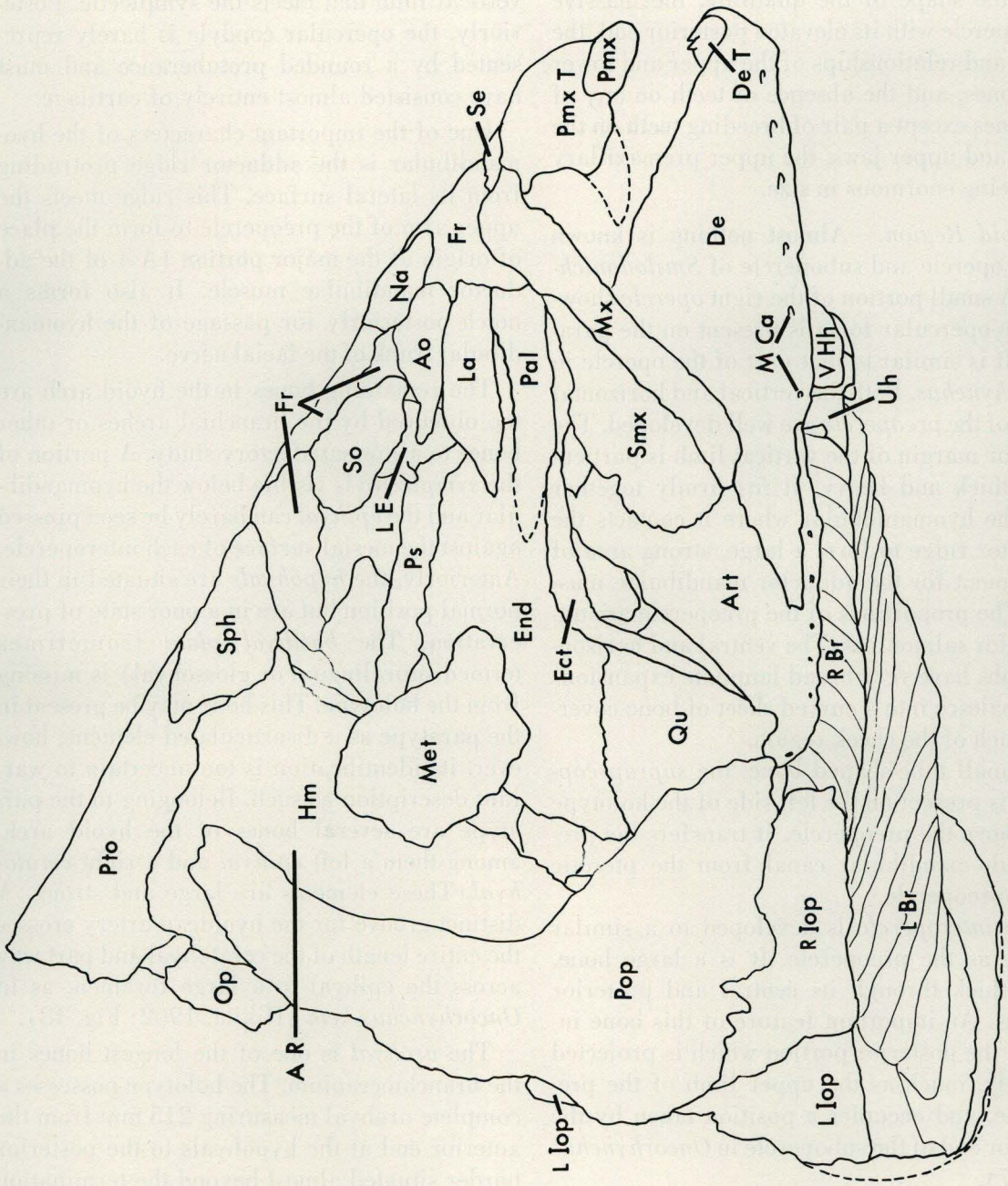


Figure 6. *Right side of articulated skull of holotype. Abbreviations are given on the page preceding Figure 3.*

usual feeding mechanism. The most important of these are the very high gill-raker number on the branchial arches, the enlarged endopterygoid, the shape of the quadrate, the massive interopercle with its elevated posterior end, the shape and relationships of the upper and lower jaw bones, and the absence of teeth on any of the bones except a pair of breeding teeth on the lower and upper jaws, the upper premaxillary pair being enormous in size.

Hyoid Region.—Almost nothing is known of the opercle and subopercle of *Smilodonichthys*. A small portion of the right *opercle* showing the opercular fossa is present on the paratype. It is similar to that part of the opercle in *Oncorhynchus*. Both the vertical and horizontal limbs of the *preopercle* are well developed. The anterior margin of the vertical limb is particularly thick and heavy. It fits firmly together with the hyomanidbular where it contacts the adductor ridge to form a large, strong area of attachment for the adductor mandibulae muscles. The proportions of the preopercle are unusual for salmonines. The ventral and horizontal limbs have very broad laminate expansions that coalesce into a curved sheet of bone covering much of the cheek region.

A small tube-shaped bone, the *suprapreopercle*, is present on the left side of the holotype just above the preopercle. It transfers the preoperculo-mandibular canal from the pterotic to the preopercle.

The *interopercle* is developed to a similar degree as the preopercle. It is a large bone, quite thick through its central and posterior regions. An important feature of this bone involves the posterior portion which is projected dorsally, much as the upper limb of the preopercle, and occupies a position taken by the anterior end of the subopercle in *Oncorhynchus* (Fig. 7).

The *branchiostegal* series appears to be complete in the holotype. There are 14 branchiostegal rays on the left side and 15 on the right. The individual rays are long, wide, and broadly overlapping.

In the suspensorium, the *hyomandibular* is the largest component. Dorsally, it has a single broad head for articulation with the neurocranium. The bone tapers ventrally into a strong vertical limb that meets the symplectic. Posteriorly, the opercular condyle is barely represented by a rounded protuberance and must have consisted almost entirely of cartilage.

One of the important characters of the hyomandibular is the adductor ridge protruding from its lateral surface. This ridge meets the upper arm of the preopercle to form the place of origin of the major portion (A_2) of the adductor mandibulae muscle. It also forms a notch posteriorly for passage of the hyomandibular trunk of the facial nerve.

The remaining bones in the hyoid arch are too obscured by the branchial arches or other bones to allow satisfactory study. A portion of the *symplectic* is visible below the hyomandibular and the *epihyal* can barely be seen pressed against the mesial surface of each interopercle. Anteriorly, the *hypohyals* are situated in their normal position but are in a poor state of preservation. The *basihyal plate* (sometimes termed supralingual or glossohyal) is missing from the holotype. This bone may be present in the paratype as a disarticulated element; however, its identification is too uncertain to warrant description as such. Belonging to the paratype are several bones of the hyoid arch, among them a left *epihyal* and a right *ceratohyal*. These elements are large and strong. A distinct groove for the hyoidean artery crosses the entire length of the ceratohyal and part way across the epihyal to a large foramen, as in *Oncorhynchus keta* (Hikita, 1962: Fig. 48).

The *urohyal* is one of the longest bones in the branchiocranium. The holotype possesses a complete urohyal measuring 215 mm from the anterior end at the hypohyals to the posterior border situated almost beyond the termination of the epihyals. In the same individual, the complete right mandible measures 265 mm long. The shape of the urohyal resembles that in *Oncorhynchus* where it is proportionately longer than in other salmonines. Nevertheless, the urohyal in *Oncorhynchus* barely reaches

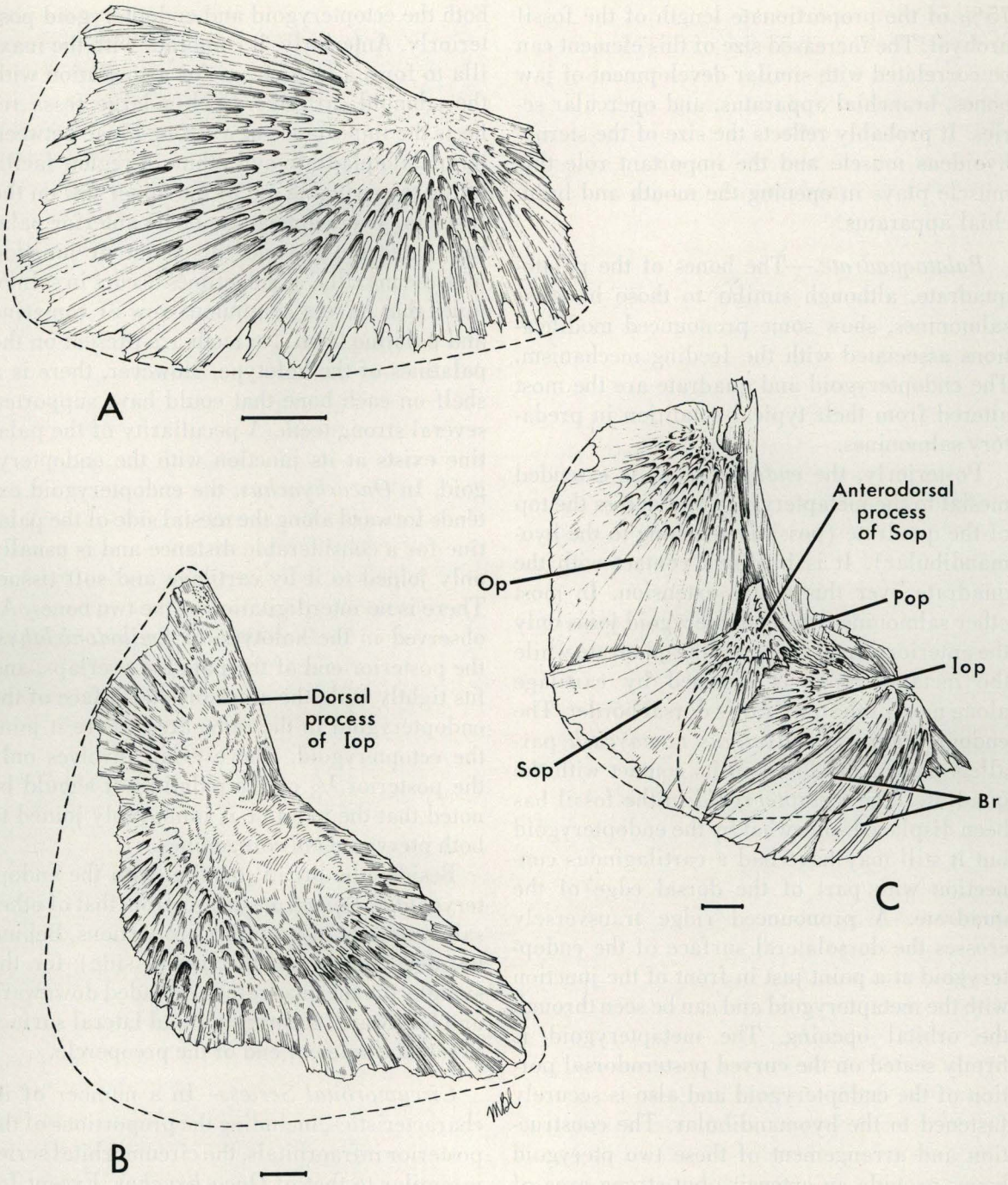


Figure 7. *Comparison of right interopercles in* Oncorhynchus tshawytscha *(A), UMMZ 178987-S, and the holotype (B). Position of the anterodorsal process of the subopercle in relation to the interopercle (with dashed margin) shown at (C), drawn from same specimen as (A) but mesial view of left side. Note the similarities between the dorsal process of the interopercle in the holotype and that of the subopercle in* Oncorhynchus. *Scale bars, 1 cm.*

75% of the proportionate length of the fossil urohyal. The increased size of this element can be correlated with similar development of jaw bones, branchial apparatus, and opercular series. It probably reflects the size of the sternohyoideus muscle and the important role this muscle plays in opening the mouth and branchial apparatus.

Palatoquadrate.—The bones of the palatoquadrate, although similar to those in other salmonines, show some pronounced modifications associated with the feeding mechanism. The endopterygoid and quadrate are the most altered from their typical condition in predatory salmonines.

Posteriorly, the *endopterygoid* is extended mesial to the metapterygoid and across the top of the quadrate (possibly reaching to the hyomandibular). It is in direct contact with the quadrate over this entire extension. In most other salmonines, the endopterygoid joins only the anterior dorsal corner of the quadrate while the metapterygoid is fastened by cartilage along most of the quadrate's dorsal border. The endopterygoid of *Salvelinus namaycush* parallels that of the fossil in its contact with the quadrate. The *metapterygoid* in the fossil has been displaced somewhat by the endopterygoid but it still may have had a cartilaginous connection with part of the dorsal edge of the quadrate. A pronounced ridge transversely crosses the dorsolateral surface of the endopterygoid at a point just in front of the junction with the metapterygoid and can be seen through the orbital opening. The metapterygoid is firmly seated on the curved posterodorsal portion of the endopterygoid and also is securely fastened to the hyomandibular. The construction and arrangement of these two pterygoid bones provide an extensive but strong area of insertion for divisions of the levator and adductor arcus palatini muscles which function in lifting the palatoquadrate arches and pulling them toward the midline, thus assisting in the closure of the mouth.

The *ectopterygoid* is present as in other salmonines. The *palatine* is rigidly united with both the ectopterygoid and endopterygoid posteriorly. Anteriorly, it combines with the maxilla to form a large fossa for articulation with the ethmoid cartilage. Such a large fossa reflects the importance of a strong hinge between the palatoquadrate and ethmoid region facilitating the swinging out of the upper jaw on the rostrum. There appears to be no anterior palatine extension beyond this point of junction with the maxilla, as sometimes occurs in salmonines that have a continuous row of vomerine and palatine teeth. No teeth are present on the palatines of the holotype. However, there is a shelf on each bone that could have supported several strong teeth. A peculiarity of the palatine exists at its junction with the endopterygoid. In *Oncorhynchus*, the endopterygoid extends forward along the mesial side of the palatine for a considerable distance and is usually only joined to it by cartilage and soft tissue. There is no interdigitation of the two bones. As observed in the holotype of *Smilodonichthys*, the posterior end of the palatine overlaps, and fits tightly with, the anterior lateral face of the endopterygoid in the same area where it joins the ectopterygoid. The overlap involves only the posterior $\frac{1}{3}$ of the palatine. It should be noted that the palatine is immovably joined to both pterygoids in coregonines.

Besides the broad junction with the endopterygoid, the *quadrate* differs from that of other salmonines in its posterior proportions. Behind the deep notch (on the mesial side) for the symplectic, the quadrate is extended downward and backward, forming a broad lateral surface to seat the anterior end of the preopercle.

Circumorbital Series.—In a number of its characteristics, including the proportions of the posterior infraorbitals, the circumorbital series is similar to that of *Oncorhynchus*. Except for a small missing piece below the eye at the lower orbital margin, the circumorbitals are intact on the left side of the holotype. There are a total of nine, one more than is usually found in *Salmo* and *Oncorhynchus*. Five infraorbital bones are situated behind the eye, the uppermost one, in this case infraorbital 7 (dermosphenotic, Nel-

son, 1969), receives the infraorbital canal from the pterotic. The next two posterior infraorbitals situated below the dermosphenotic have broken posterior ends; the fourth (infraorbital 4) extends at least 2/3 of the distance from the orbital rim to the anterior edge of the preopercle.

The slender bone carrying the infraorbital canal under the eye (infraorbital 2) is not complete as stated above. It joins the *lacrimal*, a heavy, elongate bone shaped something like a common milkweed pod. It has a blunt anterior projection and tapered posterior end. The lacrimal articulates directly, over an extended area, with another large element, the *antorbital*. Dorsal and posterior to the antorbital is a tear-shaped *supraorbital*. The form and relationships of the individual elements in the circumorbital series indicate that the eye and nares of the fossil were similar to those of other salmonines. The major difference noted is the enlargement of the three bones (lacrimal, antorbital, supraorbital) associated with the pumping mechanism of the olfactory organ (see Gosline, 1961) and the extended contact between the lacrimal and antorbital.

Mandibular Region.—The upper and lower jaw bones of the fossil are so distinctive that the species can be identified from their isolated occurrence such as at the Oregon Worden Locality (Fig. 13). In lateral view, the lower jaw has a massive appearance, being long, very deep, especially at the coronoid process, and heavy through the anterior part of the dentary. The shape is much different from the long slim jaw of *Oncorhynchus* (Fig. 8) which has a depth at the coronoid process of 20-25% of its length. Reconstructed, the depth of the fossil lower jaw is about 34% of its length. Other proportional differences are apparent in the shorter oral border of the dentary and in the longer elevated border of the articular. A linear analysis of the lower jaw is given in Figure 8.

The short oral border of the dentary can be correlated with the reduction of its dentition. One or two small teeth are seated on a brief shelf at the anterior end of each lower jaw near the symphysis. One tooth is present on UCMP 93170; a main cusp and an accessory cusp are present on each side in the holotype. A single-cusped tooth is present on the dentaries of the paratype; in addition, on the right side, there is a smaller replacement tooth seated in a reclined position behind the first. These teeth have large osseous bases fused to the dentary and resemble in certain aspects the breeding teeth in male Pacific salmon such as *Oncorhynchus keta*. Excepting the short tooth-bearing shelf, the oral border of the *dentary* is a sharp ridge which shows no evidence of bearing teeth. In contrast, the tooth-bearing shelf on the dentary in *Oncorhynchus* extends nearly the entire length of the oral border. The thick anterior portions of the fossil dentaries indicate that this area was subject to considerable stress. The anterior ends of the dentaries curve toward the symphysis. When the two bones are united at their symphysial joint, a wide interspace results. The lower jaw is quite straight, without an upturned anterior end (Fig. 8).

Another easily identifiable character of the lower jaw is the dorsal process of the *articular* which projects from behind the articular fossa and carries the mandibular canal. This process forms an angle of 30 degrees with a line drawn through the symphysis to the floor of the fossa (Fig. 8). In other salmonines, this angle is close to 90 degrees. The angle reflects the width of the articular fossa.

Upper Jaw.—When viewed from their mesial side (Fig. 9 A), the *premaxillae* show, anteriorly, flat triangular surfaces that were seated against a bluntly shaped azygous rostrum. In lateral and dorsal views (Fig. 9 B, C), the premaxilla has the appearance of a curved, wing-like bone, proportioned longer than wide and tapered anteriorly. The lateral surface is convex and faces slightly upwards. The curve of the dorsal border in the holotype inscribes a 65 degree arc of a circle 140 mm in diameter. Since the lateral surfaces of the premaxillae help mold the contour of the snout in salmonines, it is possible to obtain some idea of the

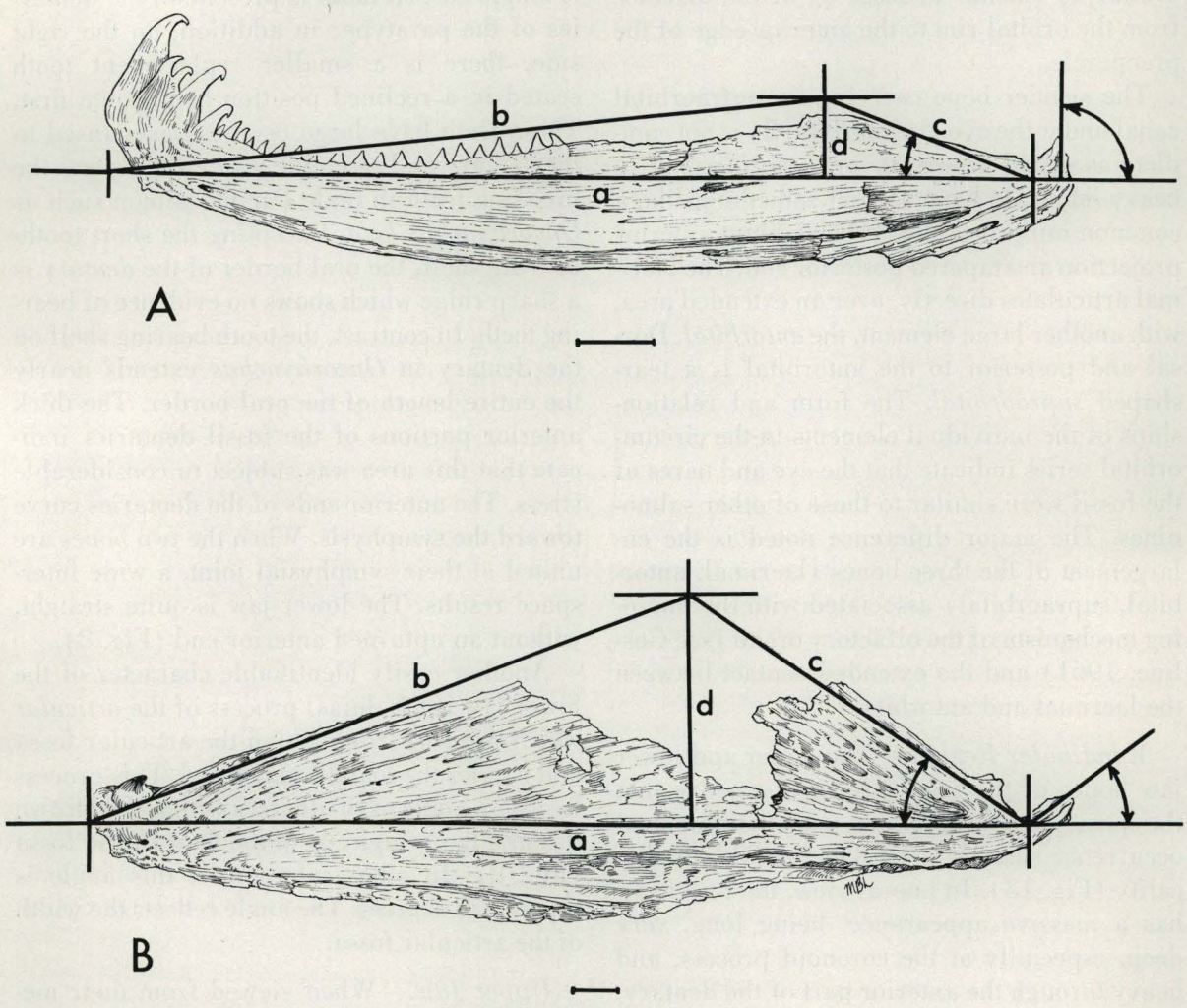


Figure 8. *Linear analysis of left mandibles in* Oncorhynchus keta *(A), UMMZ 175915-S male, and the paratype (B). a, length of mandible; b, length of oral margin of dentary; c, length of ascending margin of articular; d, height of coronoid process (determined from complete mandible of holotype); anterior angle measuring slope of ascending margin of articular; posterior angle measuring orientation of dorsal process. Scale bar, 1 cm.*

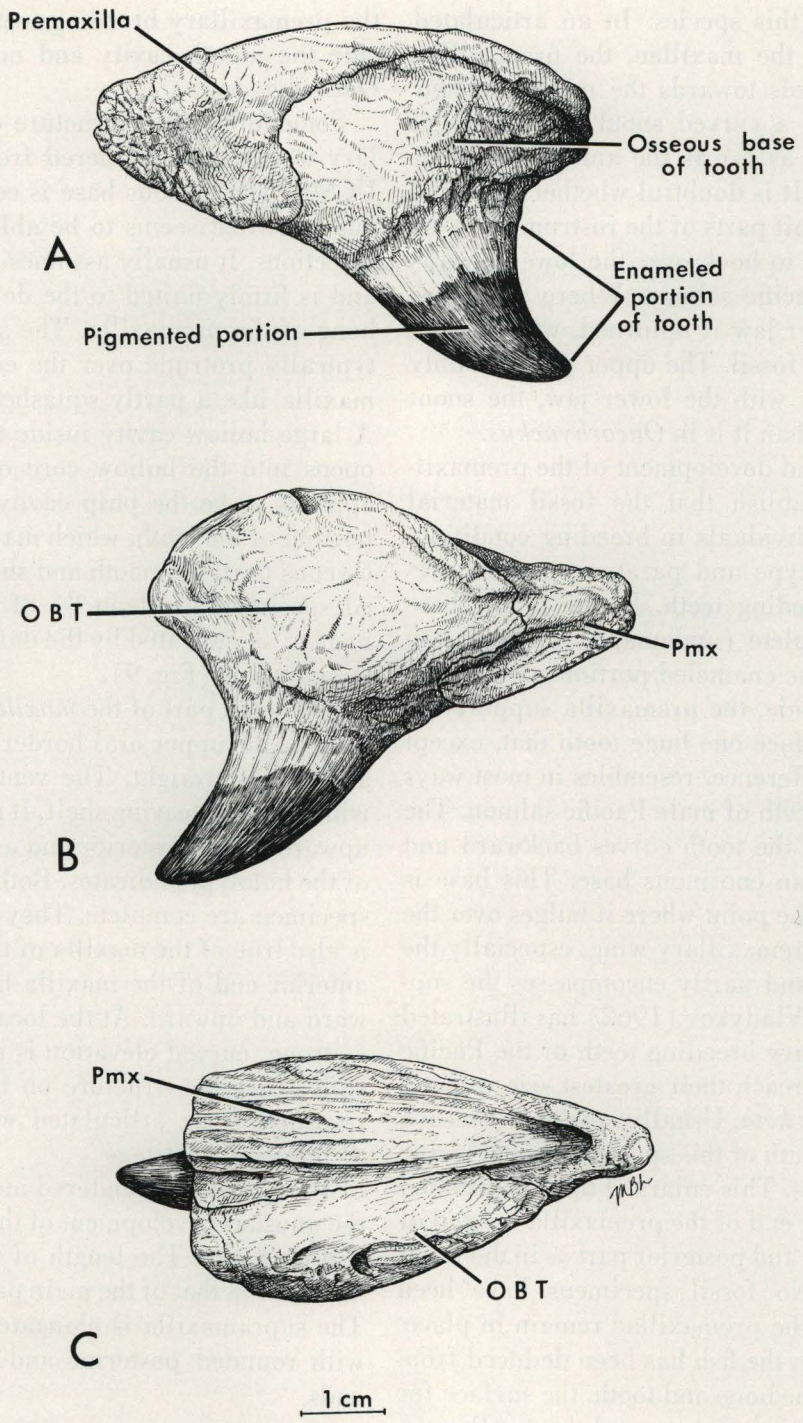


Figure 9. *Right premaxilla of paratype with breeding tooth attached. A, mesial view; B, lateral view; C, dorsal view.*

snout form in this species. In an articulated condition with the maxillae, the premaxillae curve downwards towards the midline. Their shape suggests a curved snout that extended forward about as far as the anterior limit of the lower jaw. It is doubtful whether the cartilaginous and soft parts of the rostrum were extended enough to hook over the lower jaw, as in breeding Pacific salmon. Where this takes place, the lower jaw is upturned, which is not the case in the fossil. The upper jaw probably remained even with the lower jaw, the snout being shorter than it is in *Oncorhynchus*.

The form and development of the premaxillary teeth establish that the fossil material came from individuals in breeding condition. Both the holotype and paratype possess premaxillary breeding teeth. In the latter these teeth are complete (undamaged), whereas in the holotype the enameled portions are broken off. On each side, the premaxilla supports on its ventral surface one huge tooth that, except for the size difference, resembles in most ways the breeding teeth of male Pacific salmon. The large point of the tooth curves backward and inward from an enormous base. This base is developed to the point where it bulges over the edges of the premaxillary wing, especially the lateral edge, and partly encompasses the supporting bone. Vladykov (1962) has illustrated the premaxillary breeding teeth of the Pacific salmon; they reach their greatest size in male *Oncorhynchus keta*. Usually, one tooth on each side of the mouth of this species is much larger than the others. This enlarged tooth is situated at the anterior end of the premaxilla instead of on the median and posterior part as in the fossil premaxilla. No fossil specimens have been found where the premaxillae remain in place. Orientation on the fish has been deduced from the curve of the bone and tooth, the surface for attachment to the rostrum, and the small articular surface (the only area free from the osseous base of the tooth) which met the anterior articulating process of the maxilla. The area lies on the lower side at the posteromesial corner. Based on these criteria, it is probable that the premaxillary breeding teeth were held inside the mouth cavity and not outside as in *Oncorhynchus*.

Something of the structure of the premaxillary teeth can be gathered from specimens at UCMP. The osseous base is composed of porous bone that seems to be able to grow in all directions. It usually assumes a bulbous shape and is firmly united to the dermal supporting bone of the premaxilla. The sides of the base typically protrude over the edges of the premaxilla like a partly squashed marshmallow. A large hollow cavity inside the osseous base opens into the hollow core of the tooth and appears to be the pulp cavity. The enameled portion of the tooth, which may extend into the osseous part, is smooth and shiny (in noneroded specimens). About $\frac{2}{3}$ of this part is pigmented as indicated by the dark tooth points of the paratype (Fig. 9).

The main part of the *maxilla*, which formed most of the upper oral border, is long, slender and fairly straight. The ventral edge is thin with no tooth-bearing shelf. It may turn slightly upward at the posterior end as the left maxilla of the holotype indicates. Both maxillae of this specimen are complete. They lack teeth which is also true of the maxilla of the paratype. The anterior end of the maxilla bends sharply inward and upward. At the location of the bend, a strong, curved elevation is present that joins with a similar structure on the palatine. The resulting fossa articulated with a process of the ethmoid cartilage.

The maxilla is rendered more prominent by the unusual development of the very long, deep *supramaxilla*. The length of the latter bone is about 80% that of the main part of the maxilla. The supramaxilla is elongate and tear-shaped with rounded posterior and tapered anterior ends.

Branchial Region.—The excellent preservation of the holotype has kept intact the major parts of the first three gill arches (Fig. 10). The gill rakers attached to these arches reveal much about the feeding habits of this species

and provide the most important diagnostic character for systematic description.

The branchial apparatus is twisted to the right from its normal position and is partly collapsed toward the rear due to the lateral compression of the skull during burial. The first lower arch on the right side measures about 260 mm in length, almost the same length as the lower jaw. The great length of this arch may be expressed as a proportion of the head length, which it enters about 1.8 times.

Not much can be told about the individual elements composing the gill arches since they are covered by the gill rakers. Dorsally, portions are visible of what appear to be right and left elements of epibranchial 1, pharyngobranchial 2, anterior epibranchial 2 and possibly pharyngobranchial 3. Jammed on top of the hypohyals is basibranchial 1. Extending posteriorly from it may be the anterior overlapping projection of the basibranchial plate.

In both size and number, the *gill rakers* are greatly developed. The first two lower arches are nearly complete in their gill-raker complement. Those of the first two upper arches are mostly in place but the count cannot be considered complete. The posterior parts of both third arches are missing. Table 1 gives the counts for the three arches. The gill rakers are longest at the angle of each arch, gradually becoming shorter anteriorly. On the first lower arch, the gill rakers range from about 80 mm long at the angle to 10 mm at the anterior end of the arch. On the second lower arch, the posterior gill rakers are 50-60 mm long and about 7 mm wide.

As preserved in the holotype, the arrangement of the gill rakers is particularly interesting. The distal parts of each proceeding row overlap the proximal portions of the row in front. The result is that the gill rakers blanket the inside of the branchial chamber. Individual gill rakers are strongly compressed and those of the same row are very close together, like the fine teeth on a pocket comb. Each gill raker is tapered to very slender proportions and, in its position on the gill arch, each curves slightly anteriorly. The gill rakers are smooth with no trace of denticulations so characteristic of predaceous salmonines. Such denticulations are reduced in *Oncorhynchus gorbuscha* and *O. nerka* (Hikita, 1962). The gill-raker form in these two species is closer to that of the fossil than it is to that of the other Pacific salmons.

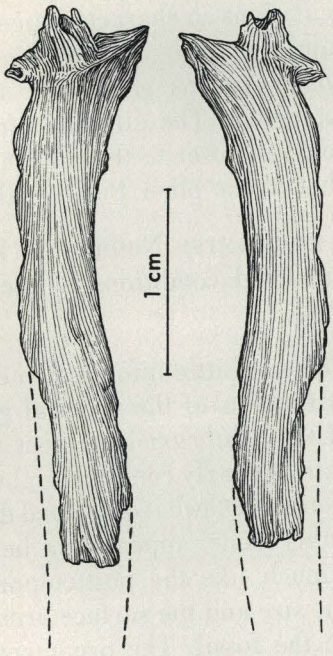
POSTCRANIAL ELEMENTS: Nothing is known about the articulated conditions of the postcranial skeleton.

Pectoral Girdle.—Little information can be gathered from remains of the pectoral girdle. A fragment of the *cleithrum* is present in the paratype and also a nearly complete right *posttemporal.* Although somewhat deformed during preservation, this bone appears to be constructed very much like the posttemporal in salmonines. The size and the surface ornamentation differ in the fossil. The ornamentation consists of fine ridges that are oriented with the long axis of the bone.

Vertebral Centra.—Both precaudal and caudal centra are associated with the skull parts of the paratype. About 40 vertebrae are represented. Neural and hemal spines are broken or missing from the caudal centra and neural spines and parapophyses are missing from the precaudal centra. The parapophyses were not fused to the centra (as in Salmonidae).

Each centrum is amphicoelous and is perforated centrally by a tiny hole. The ornamentation on the lateral surfaces of the centra consists of a minute reticulated network dominated by a series of fine longitudinal ridges. On one lateral surface between the neural arch and parapophysis on a precaudal centra, there may be up to fifteen of these ridges. Most run parallel to one another but some run obliquely. The circular ends of the centra have smooth and continuous outside margins (Fig. 11).

Among Recent and known fossil Salmonidae, the ornamentation on the vertebral centra of this species is distinctive.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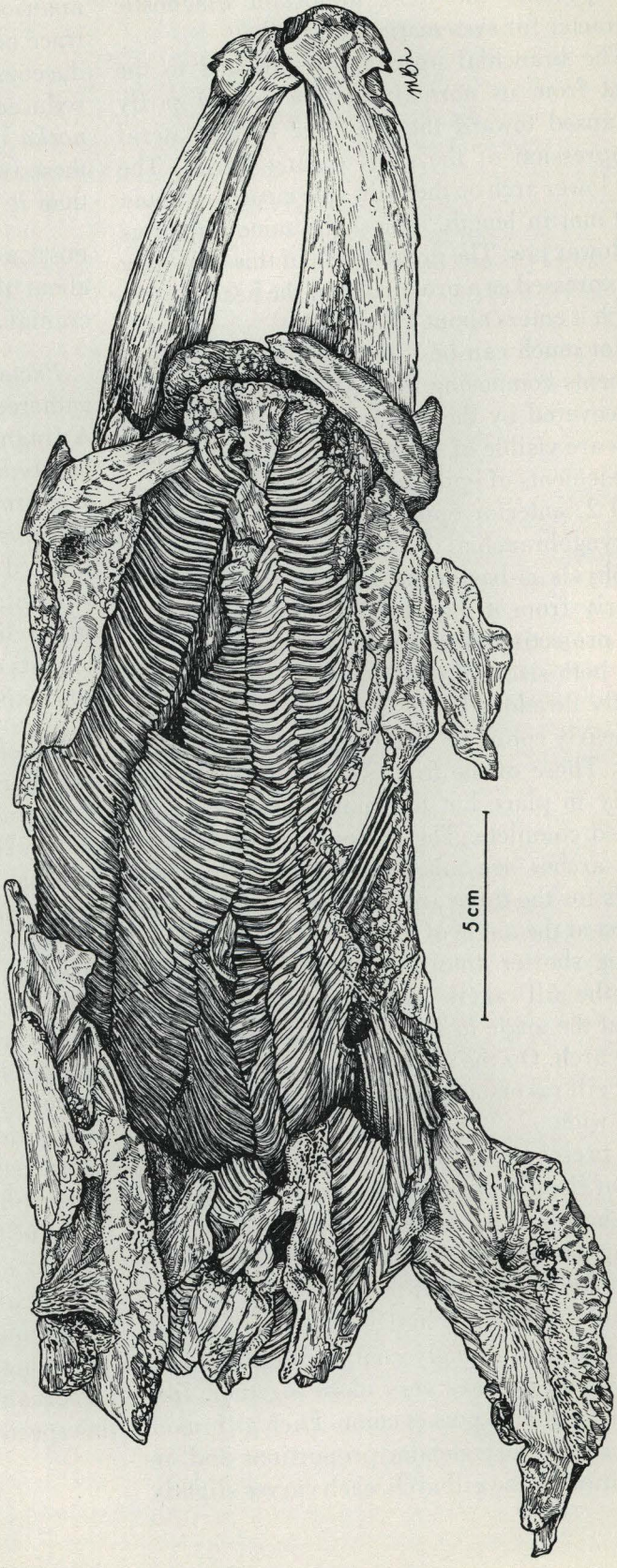
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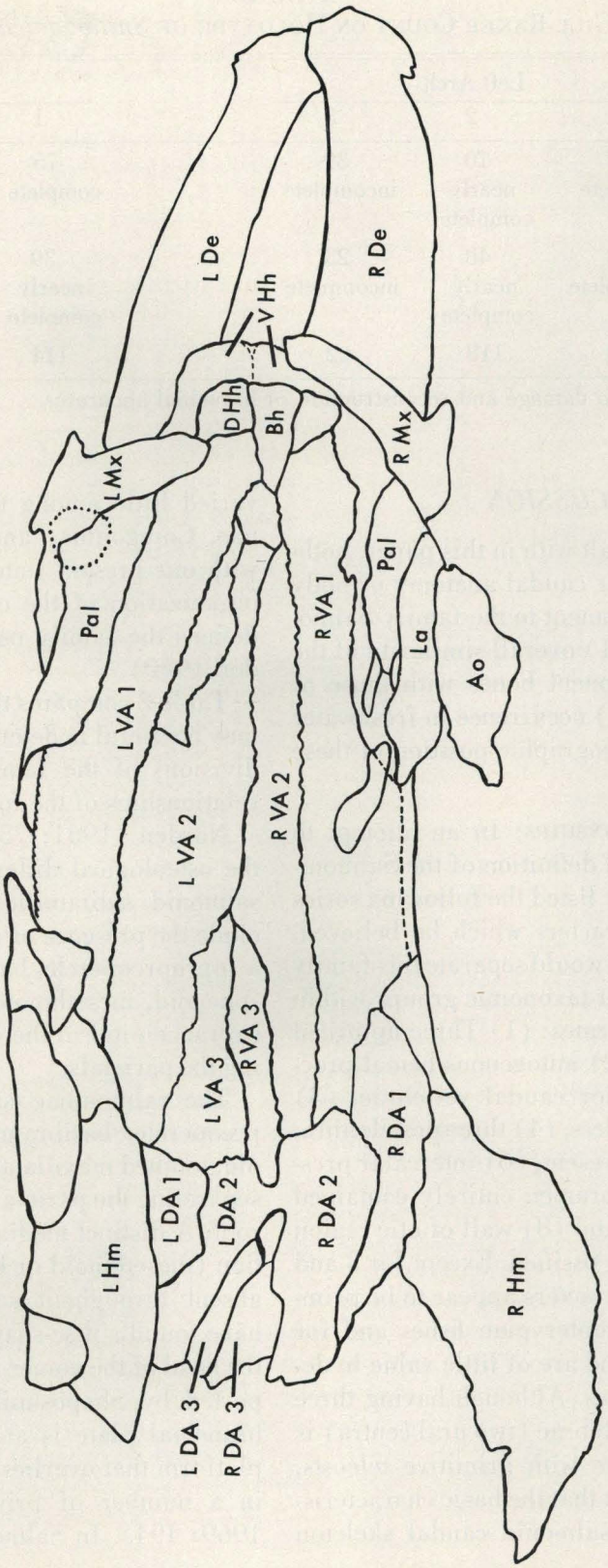

Figure 10. *Dorsal view of orobranchial chamber of holotype showing gill rakers in place. Insert shows surface detail on both sides of an individual gill raker. Abbreviations are given on the page preceding Figure 3.*

TABLE 1
GILL-RAKER COUNT ON HOLOTYPE OF *Smilodonichthys**

	Left Arch			Right Arch		
Limb	1	2	3	1	2	3
Lower	77 complete	70 nearly complete	39 incomplete	75 complete	68 nearly complete	33 incomplete
Upper	33 incomplete	48 nearly complete	23 incomplete	39 nearly complete	36 or 37 incomplete	17 incomplete
Totals	110	118	62	114	104 or 105	50

* Counts made prior to damage and reconstruction of branchial apparatus.

DISCUSSION

For the fossils dealt with in this paper, nothing is known of their caudal anatomy or body and fin form. Assignment to the family Salmonidae is based on: (1) overall similarity of the skull and its component bones with those of living salmonids, (2) occurrence in freshwater deposits, and (3) geographic position of these deposits.

SUBFAMILY RELATIONSHIPS: In an attempt to form an osteological definition of the Salmonidae, Norden (1961) listed the following series of osteological characters which he believed, when taken together, would separate this family from all other higher taxonomic groups within the order Salmoniformes: (1) Three upturned caudal vertebrae, (2) autogenous hemal processes on the posterior caudal vertebrae, (3) endopterygoid toothless, (4) three postcleithra, (5) mesocoracoid present, (6) intercalar present, (7) scapular foramen entirely contained within the scapula, and (8) wall of otic region of braincase entirely ossified. Except for 3 and possibly 7, these characters appear to be primitive for Protacanthopterygian fishes and for teleosts in general and are of little value in delimiting phyletic lines. Although having three upturned caudal vertebrae (two ural centra) is not a unique feature with primitive teleosts, Norden did point out that the basic characteristic features of the salmonid caudal skeleton varied little among the subfamilies Salmoninae, Coregoninae and Thymallinae. At least with our present state of knowledge, it is the organization of the caudal skeleton that best defines the family osteologically (see Cavender, 1970).

Table 2 compares the cranial characters that may be useful in determining the main phyletic divisions of the family Salmonidae and the relationships of the fossil to these divisions.

Norden (1961: 752-753) has summarized the osteological differences between the three salmonid subfamilies. These differences include the presence or absence of the following: a suprapreopercle, basibranchial plate, orbitosphenoid, mesethmoid, teeth on maxilla, and supraoccipital in the skull roof broadly dividing the parietals.

The Salmoninae consistently have a suprapreopercle, basibranchial plate, orbitosphenoid, toothed maxilla and a large supraoccipital separating the parietals in the back of the skull roof. A distinct median endochondral ossification (mesethmoid or hypethmoid) is typically absent throughout salmonines, although we have found a disc-shaped ossification dorsal to the head of the vomer in *Hucho perryi* (also reported by Shaposhnikova, 1968). The basibranchial plate is an elongate, tooth-bearing platform that overlies basibranchial bones 1-3 in a number of primitive teleosts (Nelson, 1969: 494). In Salmoniformes, including the

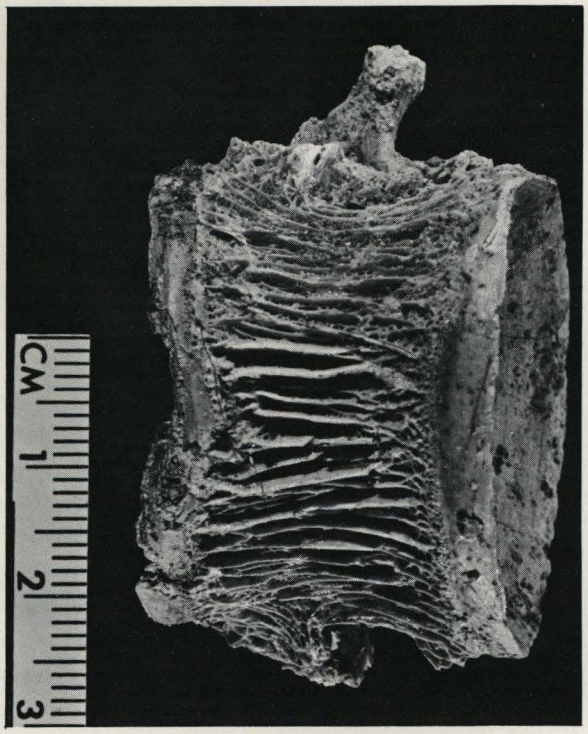

Figure 11. *Anterior caudal vertebra of parataype.*

TABLE 2

COMPARISON OF OSTEOLOGICAL CHARACTERS IN THE THREE SALMONID SUBFAMILIES WITH THE FOSSIL *Smilodonichthys*

Character	Salmoninae	Thymallinae	Coregoninae	Fossil
Suprapreopercle present	X			X
Basibranchial plate absent (lost or fused)		X	X	?
Orbitosphenoid absent		X		?
Mesethmoid (hypethmoid) typically absent	X	X		X
Maxilla toothless			X	X
Parietals widely separated by supraoccipital	X			X
Premaxilla typically oriented lateral to rostrum (at least in part)	X			X
Modified anterior jaw teeth (in spawning males)	(some species)			X
Parasphenoid with wide anterior end	X			X
Antorbital and lacrimal with broad contact	*	intermediate	X	X
Occipital condyle tripartite; first vertebra modified	X	X		

* Variable, usually a narrow contact.

Salmonidae, there have been evolutionary trends toward loss of teeth on the basibranchial plate and complete loss of identity of the plate through fusion with the underlying basibranchials (Norden, 1961). In the Salmoninae, the basibranchial teeth may be present or absent and the plate is typically fused with basibranchial 3 although the plate maintains its individuality. In the Coregoninae, the basibranchial plate is completely fused with basibranchial 3 and has lost its identity (except in *Prosopium*). Teeth are typically absent except in some ciscos (*Coregonus*, subgenus *Leucichthys*) and *Stenodus*. Norden believed that when basibranchial teeth are present in this subfamily, they are not attached (as in *Stenodus*) to the basibranchial bone, but we have found them attached in *Coregonus reighardi*.

We believe that *Smilodonichthys* is a divergent member of the subfamily Salmoninae because it shares in common with this group a number of specialized characteristics the most important of which are the large supraoccipital dividing the parietals, the form and relationship of the premaxilla and rostrum (especially the capping bone or supraethmoid on the rostrum), the absence of a median endochondral ethmoidal bone (mesethmoid), the large jaws with modified anterior (breeding) teeth, and the presence of a suprapreopercle. At this time, it is not known if the suprapreopercle is primitive for salmonids. It may have been present in the ancestral form and through subsequent evolution has been lost in the phyletic lines represented by the Thymallinae and Coregoninae but retained in the Salmoninae. Other primitive teleosts in the divisions Elopomorpha, Clupeomorpha and Osteoglossomorpha

(Greenwood *et al.*, 1966) apparently lack the suprapreopercle (see Goody, 1969: 237-239, for a recent discussion of the teleost suprapreopercle). Within the Salmoniformes it occurs only in the Salmoninae, and among the other Euteleostei a suprapreopercle is only known in certain groups of Ostariophysi (including the Gonorynchiformes according to Rosen and Greenwood, 1970). A suprapreopercle has been questionably reported by Nybelin (1962) in *Leptolepis coryphaenoides* of the basal teleostean family Leptolepidae. However, in other "leptolepids" that have been studied osteologically (Patterson, 1967; Cavender, 1970), a suprapreopercle has not been found.

The absence of a well ossified orbitosphenoid in the anterior braincase is undoubtedly a derived characteristic of the Salmoniformes (Goody, 1969; Nelson, 1969). The lack of a basibranchial plate and absence of teeth on the maxilla are specializations which may be related to a microphagous method of feeding in *Smilodonichthys*. The evolution of this form involved change from a predaceous type of feeding found in most salmonines, where prey is seized by toothed jaws, to one where jaw teeth are lost and food is strained from the water by the branchial apparatus. The result of these changes parallels in many ways the microphagous method of feeding in the Coregoninae.

It has been shown that an evolutionary trend has existed in the Salmoninae toward elongation and enlargement of the snout region with corresponding enlargement and change in orientation of the premaxillae (Cavender, 1970). The trend is correlated with feeding on large prey, especially other fishes. The premaxillae have come to earn strong support from the ethmoid cartilage through an extended lateral contact. The extreme condition is reached in *Oncorhynchus*. In the graylings and whitefishes, the premaxillae contact the ethmoid cartilage only at its anterior end. Here the premaxillae are weak but in the Salmoninae they are typically of much larger size. *Smilodonichthys* shows the premaxillary-rostral condition of the Salmoninae.

The antorbital in *Smilodonichthys* has a close association with the lacrimal. On both sides of the holotype, the antorbital connects with the lacrimal for most of its length. It barely touches the supraorbital on one side. Gosline (1961) has given a detailed discussion of the antorbital and supraorbital bones of lower teleosts. Primitively the antorbital is a sensory canal bone of the infraorbital series as found in Jurassic teleosts (Patterson, 1967) and in primitive living elopomorphs (Nybelin, 1966; Nelson, 1969). According to Gosline, the antorbital becomes associated with the supraorbital bone as an olfactory pumping mechanism. This is the condition in a number of Salmoniformes, including the Salmonidae. In coregonines, however, the antorbital retains the primitive close association with the lacrimal although the antorbital canal is lost. *Smilodonichthys* resembles the coregonines in this character; it also shares with the coregonines a similar type of lacrimal which possesses an anterior projection of bone in front of the lacrimal canal.

Salmonines possess a tripartite occipital condyle formed by the basioccipital and the right and left exoccipitals. Each of the components forms a facet for articulation with a three-faceted first vertebral centrum. The latter is slightly smaller than the centrum following and bears a complete neural arch and spine.

In *Smilodonichthys*, the occipital condyle is circular in shape, centrally concave, and forms a simple, single-faceted articulation with the vertebral column. Close inspection of the condyle shows that it is composed of a vertebral centrum fused with the basioccipital and closely united to each exoccipital. The fused centrum supported a neural arch as determined by a pair of indentations for seating such an arch on its dorsal surface. The organization of this basicranial-vertebral joint is similar to that found in *Tarpon atlanticus*, *Megalops cyprinoides* (Greenwood, 1970), *Albula vulpes*, *Osteoglossum bicirrhosum* and *Esox*. This condition is also found in most clupeoids (Ridewood, 1905), ichthyodectids (Bardack, 1965) and among the Ostariophysi. Among the Salmoni-

formes examined, it is found in *Osmerus*, *Coregonus* and *Stenodus*. Apparently in many lower teleosts (and holosteans as well [Rayner, 1948]), the exoccipitals do not form part of the basicranial-vertebral joint. A survey made in this study on UMMZ skeletal collections, shows that the most common type of basicranial-vertebral joint among malacopterygian fishes consists of a simple articulation between two vertebral discs, belonging to the first centrum and a "half" centrum fused to the basioccipital. In fact Ridewood (1904) concluded that this is the type of articulating surface found throughout the lower teleosts. Greenwood (1968) found a tripartite condyle in *Denticeps*, where the first centrum is not fused with the basioccipital. He considered this an evolutionary stage that must have preceded that found in most lower teleosts today. Elsewhere in the Euteleostei a tripartite condyle is found in the extinct *Enchodus*, *Apateodus*, *Halec* (Goody, 1969) and is commonly encountered in the Perciformes. Rosen and Patterson (1969) suggested that the primitive condition of the occipital condyle in Paracanthopterygii is a tripartite structure with a central notochordal pit. In Coregonines (except *Prosopium*) a vertebral centrum fused with the basioccipital typically forms the occipital condyle. The fused centrum may bear an arch or spine. Sometimes in *Coregonus* two centra may be fused with the basioccipital. Graylings possess a tripartite condyle as in salmonines. The condition in *Prosopium williamsoni* is somewhat intermediate since the exoccipitals partially enter into the articulating surface.

It appears that when a vertebral centrum becomes fused with the braincase, it usually does so for the most part primarily with the basioccipital and not with the exoccipitals, since the original basicranial vertebral articulation was with that first bone. If the exoccipitals are in contact with the fused centrum, as in *Smilodonichthys*, there is a definite line of junction visible between the exoccipital and the centrum. This is not true of the basioccipital where the line of junction with the centrum is completely obliterated in the fusion process. The different basicranial-vertebral joints found within the Salmonidae might be explained by the difference in feeding mechanisms. A fish with a powerful bite, such as a salmon, utilizes a flexible tripartite basicranial-vertebral joint (Tchernavin, 1953). A fish with small, weak jaws, such as *Coregonus*, apparently does not need this enhanced cranial-vertebral flexibility. Also, because there is no lifting of the neurocranium in biting, this area is not subject to stresses that otherwise might exist at the contact between the basicranium and the vertebral column. It is interesting to note that both in *Stenodus* and the fossil, two types with fairly large powerful jaws, the cranial-vertebral joint is simple. However, in the fossil the basioccipital facet has formed from a fusion of the proatlas centrum with the basioccipital. This centrum bears a neural arch, as it does in *Stenodus*. The fusion is not so complete that the centrum does not maintain its individuality. Moreover, the line of fusion is clearly marked by a sharp ridge. In width this centrum is narrower than those following but, nevertheless, is much wider than what would be considered a half centrum. With respect to this character in *Smilodonichthys*, evolution appears to have proceeded from the tripartite type characteristic of the Salmoninae to one where the basicranial-vertebral joint is simple. In most other lower teleosts the evidence indicates that the simple cranial-vertebral joint is the primitive state.

GENERIC RELATIONSHIPS: The characters of *Smilodonichthys* discussed in the following paragraphs have a bearing on the generic classification of this species within the Salmonidae (Table 3). As this table illustrates, the fossil shares nine of the 21 listed characters with *Oncorhynchus* and only one of these is shared with other salmonines. Four characters agree with the Coregoninae. This leaves seven distinctive traits, of which the most important are: the high number of gill rakers, absence of gill-raker teeth, a keeled parasphenoid, a strong dorsal process on the interopercle, and the enlarged supramaxilla. *Smilodonichthys* further

TABLE 3

COMPARISON OF OSTEOLOGICAL CHARACTERS BETWEEN *Smilodonichthys* AND SOME OTHER SALMONID GENERA

Character	*Smilodon-ichthys*	*Onco-rhynchus*	*Salmo*	*Salve-linus*	Core-gonines
Rostral cartilage azygous (not forked)	X	X			
Supramaxilla greatly enlarged	X				
Premaxillary breeding teeth much enlarged	X	*(O. keta)*			
Mandible with high coronoid process	X				X
Dorsal process of articular obliquely oriented	X				(except *Stenodus*)
Cephalic sensory canal with many small pores	X				
Preopercle with well developed horizontal limb	X				X
Anterior process of intercalar reaching pterotic	X	X	(except *S. gairdneri*)	(except *S. alpinus*)	
Anterior part of parasphenoid exceptionally broad (spatulate)	X	X			
Posterior myodome strongly compressed	X				
Supraethmoid triangular, usually notched posteriorly	X	X	(subgenus *Parasalmo*)		
Posttemporal fossa small	X				
Interopercle with strong dorsal process	X				
Branchiostegal rays over 15	X	X			
Gill rakers over 100	X				
Gill rakers long and compressed	X				(subgenus *Leucichthys*)
Gill rakers without teeth	X	(teeth reduced in some species)		(teeth reduced in some species)	
Adductor ridge of hyomandibular well developed	X	(some species)			X
Most cranial bones highly cavernous	X	X			
Laminar parts of dermal skull bones expanded and with fimbriate margins	X	X			
Lower jaw hooked in spawing male		X	X	(some species)	

stands apart among the Salmoninae by possession of the toothless maxilla and enormous premaxillary breeding teeth.

The premaxilla is an elongate, wing-shaped bone that is slightly curved (convex side faces dorsally), most likely to conform to the shape of the snout. There is no anterior ascending process. The mesial side of the bone is flat, without any articular fossa. This side was intimately bound to the cartilaginous rostrum, a conclusion that can be reached after comparing the fossil premaxilla with that of other salmonines. Only *Oncorhynchus* among Recent salmonids possesses a premaxilla similar to the above type. Its characteristics, along with those of the snout, clearly separate *Oncorhynchus* from other salmonines. The latter all possess a premaxilla with an anterior articular fossa on its

mesial side which receives a cartilaginous knob protruding from each side of the rostrum (labial cartilage of Tchernavin, 1938, 1943). The rostrum in *Oncorhynchus* is azygous, without protruding cartilages. In addition this genus has an extended area of attachment for the posterior wing of the premaxilla.

A toothless condition of the maxilla has occurred a number of times in the evolution of the Salmoniformes, both in conjunction with microphagous and piscivorous adaptations of the jaws and teeth. When piscivorous, the maxilla tends to be excluded from the gape by an enlarged premaxilla and the palatines tend to form a powerful dentition that becomes a major part of the bite. Examples can be found in the esocids, galaxioids, and the extinct *Apateodus, Cimolichthys, Enchodus* and *Eurypholis pulchellus* (Goody, 1969). Among the Salmonidae, the predaceous types possess strong maxillary teeth but these teeth have been lost in the microphagous feeders, such as the Coregoninae. *Smilodonichthys* has no trace of the maxillary teeth, although the bone itself enters a large part of the gape. The oral border is slightly convex (suggestive of the condition in the coregonines) which appears to be a primitive teleostean feature.

Besides the toothless oral border of the maxilla, a further distinctive feature of the upper jaw of *Smilodonichthys* is the exceptionally large supramaxilla. This bone is usually an elongate structure positioned along the dorsolateral part of the maxilla in salmonines. In *Salvelinus* it is very slender but in *Salmo* and *Oncorhynchus* a deep laminal portion extends down over the outer side of the maxilla. The supramaxilla is deepest in *Oncorhynchus*, where it is similar in form to that of *Smilodonichthys*. None of the living salmonines possess a supramaxilla of the size found in this extinct genus. Nor do we know of any teleost possessing a supramaxilla of comparable size.

The possession of modified anterior jaw teeth in anadromous breeding male individuals of some salmonine species, such as *Salmo salar, Salmo trutta, Salvelinus fontinalis* and all members of the genus *Oncorhynchus*, is a highly specialized feature for teleostean fishes. These breeding teeth are a secondary sex character best developed in the largest mature spawning males of those forms that migrate upstream to spawning areas. Their function appears to be in display and fighting behavior between male individuals for possession of females and territory as well as display in mating with the female. Among living Salmoninae, the breeding teeth reach their largest size in members of the genus *Oncorhynchus*. In *Smilodonichthys* the premaxillary breeding teeth have reached an extreme size, so large that there is room for only one tooth on each side of the snout.

The black pigmentation of the tips of these breeding teeth appears to be a further specialization, perhaps accentuating the display behavior of the breeding male. Large black teeth are found in *Smilodonichthys* (both those of the premaxilla and dentary) and in certain species of *Salmo* (Tchernavin, 1943).

A stout mandible with a high coronoid region is found in *Smilodonichthys* and the Coregoninae among the Salmonidae. This type of mandible is characteristic of umbrids, clupeoids, some elopoids, ichthyodectids and leptolepids. It may be primitive for at least some of the lower teleosts. A similar lower jaw also occurs in the pholidophorids. Dimensions of the *Smilodonichthys* lower jaw are indicated in Figure 8. There is a large area on its mesial side for insertion of the adductor mandibulae muscle. There was little encapsulation of the muscle anteriorly by the dentary. An unusual feature of the lower jaw is its open articular fossa. Typically in salmonines a dorsal process of the articular forms the posterior enclosure of the articular fossa. This process is bound to a ridge on the posteroventral margin of the quadrate by a strong ligament. The articular fossa is deep and narrow and closely bound to the articulating condyle on the quadrate.

In *Smilodonichthys* the dorsal process of the articular is well developed but unlike the condition in other salmonines it is directed ob-

liquely backward, paralleling the posteroventral elevation on the quadrate. It is likely that a strong ligament joined the articular process to the ridge of the quadrate but there also may have been a ligamentous connection with the anterior end of the preopercle. Among the Salmonidae, a wide open articular fossa is found in *Stenodus* and will be commented on later. The function of such a fossa probably has to do with increasing the drop of the lower jaw to a level exceeding that of typical salmonines. In the latter, a strong bite is present which necessitates a firm joint between the articular and quadrate to prevent dislocation.

In addition to the suprapreopercle, two distinguishing characteristics of the cephalic sensory canal in *Smilodonichthys* are the number and size of the openings to the surface of the bone. This is particularly noticeable in the supraorbital canal where there are 11 or 12 openings in each frontal. The pores are minute and elevated above the frontal surface indicating that the skull roof was covered by a fairly thick layer of skin and soft tissue. The preoperculo-mandibular canal also carries many small pores, about 11 on the preopercle and 13 on the lower jaw. The preopercular canal pattern further differs from other salmonids in having a number of posterior branches, as found in certain early teleosts (Patterson, 1967) and in pholidophorids (Nybelin, 1966). The preopercular bone itself has a well developed horizontal limb which is unusual for salmonines but typical for smaller-mouthed salmonids such as *Thymallus* and coregonines. A similar type of preopercle is probably primitive for teleosts, as recently discussed by Gardiner (1967).

In most living teleosts where a separate intercalar is present in the neurocranium, this bone is found to cap the posterolateral corner of the braincase and serve as a place of attachment for a ligament from the pectoral girdle (posttemporal). In a number of holostean fishes, Rayner (1948) has shown that the intercalar functions in an additional manner, i.e., by forming that part of the posterior otic wall extending from the corner of the braincase to the prootic. A few lower teleosts belonging to the Elopoidei, Characoidei, and Clupeoidei also have the intercalar forming part of the otic wall. Greenwood (1970) has given a detailed description of the complex intercalar of the Megalopidae where it is involved in the swimbladder-skull linkage. Among the Salmonidae a process of the intercalar extending forward in the otic wall to the prootic has been found only in the subfamily Salmoninae (certain species of *Oncorhynchus*, *Salmo* and *Salvelinus*). The intercalar appears to be best developed in *Oncorhynchus*. *Smilodonichthys* has a relatively large extension of the intercalar into the otic wall. It sutures anteriorly with the prootic. Its external surface appears as a flat lamina without any ridges or other modifications. The main part of the intercalar at the corner of the braincase, however, is modified into a posterolaterally directed process. In the majority of salmonines, in coregonines and in *Thymallus*, the intercalar is a simple cap-like structure. It is likely that the condition in *Smilodonichthys and Oncorhynchus* is close to the primitive state for salmonids.

The ventral profile of the neurocranium as dictated by the parasphenoid can be useful in distinguishing salmonid taxa. Even taking into account that the neurocranium in *Smilodonichthys* is somewhat collapsed dorsoventrally, because of the disintegration of the cartilage interspaces between ossifications, the profile appears quite shallow in lateral and posterior view. This is supported by the flat aspect of the frontals and the lack of a strong arch in the parasphenoid. In *Oncorhynchus*, the parasphenoid is strongly arched, the frontals slope down from the midline, and the neurocranial profile is deep. *Salmo gairdneri* also has a deep neurocranial profile, but it is much shallower in *Salmo clarki*.

The keeled shape of the posterior part of the parasphenoid is one of the most derived osteological characters of the genus *Smilodonichthys*. The usual condition exhibited by salmonids with respect to this character is one in

which the posterior extension of the parasphenoid under the braincase forms, with the basioccipital and prootics, a rather broad and spacious cavity called the posterior myodome. In front there is a large opening to the myodome where the ascending wings of the parasphenoid extend dorsally to contact the prootics and a small opening posteriorly below the occipital condyle. The portions of the parasphenoid forming the sides of the myodome are somewhat flattened and the floor is gently rounded. In *Salvelinus* and *Hucho*, the myodome tends to be shallower than in most *Salmo*, *Oncorhynchus* and coregonines. *Smilodonichthys* differs in having portions of the parasphenoid that form the sides of the myodome deepened and compressed together. Thus there is a sharp angle instead of a curved floor to the myodome and the intervening space between the walls is much restricted. A keeled parasphenoid is found in many clupeoid fishes (Svetovidov, 1964), but the similarity with *Smilodonichthys* does not extend to any other features of this bone. Among extinct forms assigned to the Salmoniformes (Goody, 1969), a keeled parasphenoid occurs in the Enchodontoidei, *Enchodus lewesiensis* (Mantell) and *Eurypholis pulchellus* (Woodward). The compression of the parasphenoid posteriorly in *Smilodonichthys* may provide more space for expansion of the upper pharyngeals or it may provide increased area for attachment of muscle and supporting soft tissues associated with the operation of the gill arches.

Considerable lateral expansion of the anterior part of the parasphenoid seems to be a distinguishing trend found within the Salmoninae. Among living forms the expansion varies from slight in *Brachymystax* to well developed in *Oncorhynchus*. Extreme development of this character is reached in *Smilodonichthys*. Coregonines and *Thymallus* possess a slender to moderately developed anterior parasphenoid as do other Salmoniformes: Stomiatoidei (Weitzman, 1967), *Plecoglossus* (Chapman, 1941), *Argentina* (Chapman, 1942), and Galaxoidei (McDowell, 1969). An expanded parasphenoid is found in the myctophoid *Aulopus filamentosus* (Goody, 1969), in *Umbra* and *Dallia* of the Esocoidei (Cavender, 1969), in the osteoglossiform *Arapaima* and in some Cypriniformes. A parasphenoid expansion may take place in connection with a depressed braincase as in *Dallia* and in catfishes (Siluriformes). In the case of the Salmoninae, it probably helps to support an extended cartilaginous rostrum and an enlarged and elongated tooth-bearing vomer as in *Salmo* and *Oncorhynchus*.

A triangular supraethmoid covered the ethmoid cartilage in *Smilodonichthys*. The bone is sharply pointed at its anterior end and slightly longer than its posterior width. A notch may have been present in its posterior margin. The form of this bone is most similar to that of *Oncorhynchus* among the salmonines. That genus has a triangular supraethmoid with a posterior notch. Other salmonines, except *Salmo obtusirostris*, have an elongate supraethmoid. The notch is characteristic of native *Salmo* and *Oncorhynchus* from western North America and the North Pacific Basin. It is also found in *Salmo ohridanus*. In a previous statement, it was pointed out that there has been an evolutionary trend in the Salmonidae to elongate the supraethmoid. *Oncorhynchus* may exhibit a more primitive condition with respect to this character.

The posttemporal fossa is variously developed in areal extent among fossil and Recent Salmoniformes. Primitively (at least in the Teleostei) the fossa was probably completely roofed over by the parietals and pterotic. Weitzman (1967) and Goody (1969) have recently discussed the evolution of the posttemporal fossa in salmoniform fishes. An evolutionary trend in the group has been toward enlargement of the fossa and loss of any roofing by the parietals, pterotics or extrascapulars. In living salmonines, the fossa is entirely open above. The cavity usually extends forward onto the posterior margin of the frontal. Its floor is covered by the pterotic laterally and by the cartilage ventrally. The dorsomesial margin of the

fossa is formed by the parietal, a part of which still covers a small anterior area of the fossa. The epaxial body muscles that insert in the posttemporal fossa bury most of the dorsal portion of the pterotic in salmonines, including *Oncorhynchus*. Only a narrow ridge of the pterotic bone forming the lateral wall of the fossa and carrying the supratemporal sensory canal extends above the muscle mass. In *Smilodonichthys* the fossa is a very shallow cavity of limited extent but entirely open above. The floor appears to be formed completely of bone without intervening cartilage. The small size of this fossa is explained by the fact that it has not extended as far forward as in other salmonines nor has it eroded into most of the dorsal part of the pterotic. A considerable area of this bone was exposed to the surface and not covered by the inserting muscle mass. The small and shallow depth of the posttemporal fossa in *Smilodonichthys* appears to be a primitive feature, since an evolutionary trend in the subfamily often has been toward an enlargement of the fossa in forms with large jaws and teeth. The small size of the fossa may also be correlated with the simple type of basicranial-vertebral joint.

A bone associated with the articular of the lower jaw is the interopercle. A strong ligament joins the posterior margin of the articular with the anterior end of the interopercle. All salmonids possess an interopercle—in which the height is typically less than its length (except possibly in some *Oncorhynchus*)—as appears to be true of most lower teleosts. A deep interopercle is found in the myctophoid *Aulopus filamentosus* (Goody, 1969). Among the extinct suborders Cimolichthyoidei and Enchodontoidei, discussed by Goody (1969), the interopercle is absent. These are large-jawed predators with strong teeth. In *Smilodonichthys* the shape of the interopercle with its strong dorsal process is unique among salmonids and apparently exceptional among most other lower teleosts. We suggest that the peculiar interopercle of *Smilodonichthys* is associated with the operation of the lower jaw and the expansion of the branchial cavity.

There is a total of 29 branchiostegal rays in the holotype of *Smilodonichthys* (14 on the left and 15 on the right side). Salmonid species with this many branchiostegals are found only in the Salmoninae. Coregoninae have up to 12 on one side (*Stenodus*). *Salvelinus* usually has 10 to 12 on each side but may have an extreme of 31 rays (15 right, 16 left) in the interior western North American form of *S. "malma."* Norden (1961), Rounsefell (1962), and McAllister (1968) have summarized branchiostegal ray counts in salmonids. Of all the salmonid genera, *Oncorhynchus* possesses the highest counts, up to 19 or 20 on one side. *Hucho* has up to 14 and *Salmo* 13. *Smilodonichthys* appears to be closest to *Oncorhynchus* and *Salvelinus* in this character. McAllister (1968) concluded that the higher branchiostegal-ray counts were most likely primitive for the Salmonoidei. A similar conclusion was reached by Nelson (1970) for clupeoids. In *Smilodonichthys* the branchiostegal formula is 9-1-5, with 5 supported by the epihyal, 9 by the ceratohyal, and 1 articulating with the cartilage between these two bones.

Smilodonichthys has upwards of 110 gill rakers on the first arch. The number is probably not complete for there are more than this on the second arch, which is better exposed than the first and easier to count. This is an exceptionally high number for a salmonid as it exceeds the highest known number by more than 30. *Coregonus muksun*, a species of the subgenus *Coregonus* living in northern and western Siberia, has been reported by Himberg (1970) to range as high as 78 gill rakers. *Prosopium* may have up to 45 in *P. gemmiferum* (Norden, 1970), *Stenodus* has a maximum of about 30, 32 in *Salmo* (*S. obtusirostris*, Behnke, 1968), *Brachymystax* 31 (Shaposhnikova, 1968), *Hucho* 19 (Shaposhnikova, 1968), *Salvelinus* 33 (Berg, 1948) and a maximum of 42 in *Oncorhynchus* (Hikita, 1962). The upper limit for the number of gill rakers on the first arch in the

Salmoninae is close to 40 and almost twice that number in the Coregoninae. *Thymallus* has a maximum of 33 gill rakers (Berg, 1948). *Smilodonichthys* has a greater resemblance to the Coregoninae in its numerous gill rakers.

Those teleosts that possess a great number of closely spaced, long and attenuated gill rakers are in most cases adapted for feeding on planktonic organisms. Examples can be found in the Clupeiodei, Scombroidei, Chanoidei, Cyprinoidei, Characoidei, Elopoidei, Atherinomorpha, and Carangidae.

The length and spacing of individual gill rakers may indicate as much about the diet as does the number (Kliewer, 1970). Among the species of *Prosopium*, *P. gemmiferum* is a planktonic feeder with the longest and greatest number of gill rakers of any species in that genus. Unlike *Smilodonichthys*, however, the gill rakers of *P. gemmiferum* are well equipped with many small teeth (Norden, 1970). Those coregonines in the subgenus *Leucichthys* that are characteristically planktonic feeders, such as *Coregonus artedii*, have long, tapered gill rakers equipped with many small teeth. These teeth form an interlocking mesh as illustrated by Vladykov (1970, Fig. 13). The same is true of *Allothunnus fallai* (Tominaga, 1966, Fig. 2 B) of the Scombroidei.

In *Smilodonichthys* the large number of long, attenuated rakers, their toothless condition and closely spaced and overlapped arrangement, plus the elongation of the rows, suggest a feeding method adaptable to small pelagic organisms such as are now present in the North Pacific Ocean. The special features of this feeding mechanism and the geographic location of the fossil leave little doubt that this species fed in the ocean during its life history.

Among the Salmonidae a well developed (laterally projecting) adductor ridge of the hyomandibular is found in the Coregoninae, Thymallinae and sporadically through the Salmoninae where it occurs in *Brachymystax* and in some species of *Oncorhynchus* and *Salmo*. Elsewhere among lower teleosts it is variously developed but particularly noticeable in *Elops*, *Tarpon*, and *Esox*. The ridge appears in the Myctophiformes, Percopsiformes, Beryciformes and widely through the Perciformes. The adductor ridge is assumed to be a primitive character where it occurs in the Salmonidae including *Smilodonichthys*.

The dermal bone structure in *Smilodonichthys* combines a highly cavernous internal organization throughout the thicker portions of the bone with very thin laminate-like marginal areas. The latter are expanded in the bones of the cheek region such as the posterior infraorbitals, preopercle, and interopercle, and probably also in the opercle and subopercle. Due to the delicate nature of the peripheral parts of these expanded areas, preservation was poor. What sections remain, as on infraorbital 3, indicate that the margins were not entire but fimbriate as in *Oncorhynchus*.

The cavernous internal structure is nicely displayed in bones that have been fractured transversely to the longitudinal course of the trabeculae such as the right interopercle of the holotype. Here the cross section of the bone has the apperance of a honeycomb with numerous partitions enclosing interstices. The total effect is probably one of lightness plus strength. Other salmonines exhibit this type of dermal bone structure but to a lesser degree. Transverse sections were made through the anterior dentaries of *Smilodonichthys*, *Oncorhynchus*, and *Salmo* for the purpose of comparison (Fig. 12). It is readily apparent that the cavernulous condition of *Oncorhynchus* exceeds that of *Salmo* and approaches the condition in *Smilodonichthys*. Various authors have remarked about the fat storage ability of muscle and bone in anadromous *Oncorhynchus*. The unusual structure of the fossil bone described here might be correlated with anadromous behavior.

The lower jaw of large male salmonines in spawning condition is often curved upward or hooked at the tip (Morton, 1965). This hook or kype is both the result of growth of the dentary bone at the symphysial region and addition of soft tissues dorsal to the symphysis. Tchernavin (1943, in reference to *Salmo*

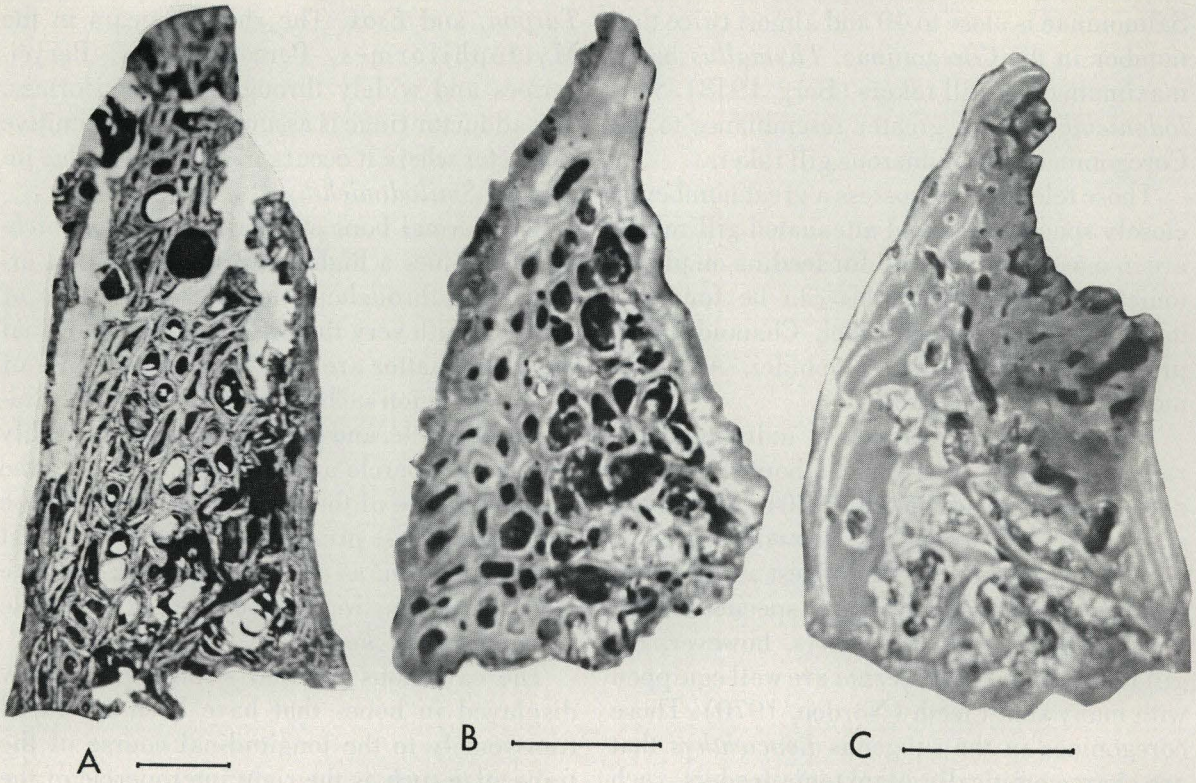

Figure 12. *Transverse sections of dentaries showing bone structure. A,* Smilodonichthys rastrosus, *UCMP 93170; B,* Oncorhynchus tshawytscha, *UMMZ 178987-S male; C,* Salmo trutta, *UMMZ 175169-S male. Scale bar, 0.2 cm.*

salar) stated that the extent of the kype is mainly dependent on the size of the individual but it is also better developed in anadromous than in resident populations of the same species. UMMZ collections include examples of male fish with hooked lower jaws among the following species: all North American species of *Oncorhynchus*, *Salmo trutta*, *S. gairdneri*, *S. aguabonita*, *Salvelinus fontinalis*, *S. alpinus* and *S. malma*.

The absence of any apparent modifications in the symphysial area of the lower jaw of individuals believed to be males in spawning condition, indicates that no kype was developed in *Smilodonichthys*.

Comparison with Stenodus.—A fruitful comparison can be made between the fossil and *Stenodus* because of certain important cranial characters shared by both genera. *Stenodus* is a fairly large-mouthed predaceous genus that is believed to have evolved from a smaller-mouthed microphagous feeder like *Coregonus* (Norden, 1961). The primary evidence for believing this is that *Stenodus* has lost its maxillary teeth and that it possesses an enlarged branchial apparatus with long, finely toothed gill rakers. The toothless maxilla unites all the Coregoninae but can no longer be regarded as diagnostic for this subfamily if the toothless character of the fossil maxilla proves to be constant. In *Stenodus*, the oral margin of the maxilla is convex, the supramaxilla is large, and the mouth opening is slightly superior. The anterior ends of the maxillae bend sharply inward and have rounded articular surfaces for efficient rotation on the palatine and rostral cartilages. The lower jaw is particularly interesting because it shares with the fossil: a nearly

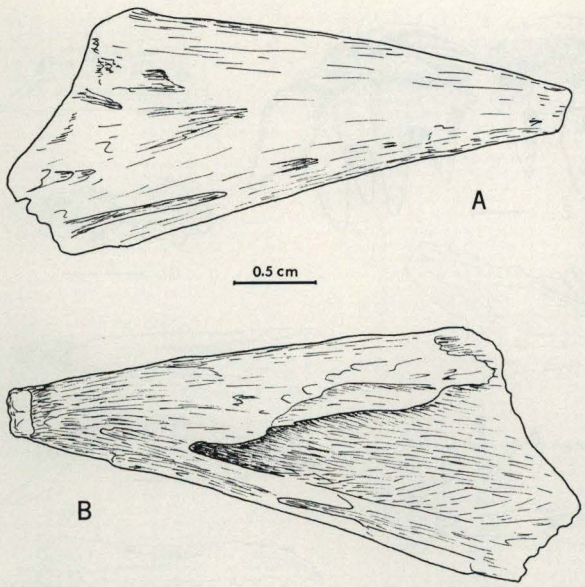

Figure 13. *Right dentary referred to* Smilodonichthys, *from Worden Locality, UMMP V58064. A, lateral view; B, mesial view.*

straight ventral border, a high coronoid process, a large area for Meckel's cartilage and the insertion of the mandibular portion of the adductor mandibulae muscle, a similarly placed corono-meckelian ossification, a heavy construction of the dentary, teeth present only near the symphysis, a pronounced inward curve of the anterior end of the dentary, and an open articular fossa. The articular has a tube-like posterior projection that receives the preoperculomandibular canal. Other characters of *Stenodus* of interest in reference to the fossil are its large preopercle with well developed horizontal arm, and the long, tapered gill rakers, mostly with denticulations.

The agreement in features of the mouth and gill rakers between *Stenodus* and the fossil indicates similarities in the method of feeding. However, this may not be the only explanation. Some of the osteological characters which in the past have been used to divide the salmonines and coregonines break down in this comparison. This is further evident in the branchiostegal count of *Stenodus*, highest among the Coregoninae, the large, heavy orbitosphenoid, and the parietals partly divided by the supraoccipital. Boulenger (1895) recognized some of these intermediate characters in *Stenodus*. The complete circumorbital ring in *Stenodus* appears to be a very primitive character in teleost fishes (Gosline, 1965), as well as its completely toothed tongue and basibranchials (Nelson, 1969; Vladykov, 1970). It is suggested here, in light of evidence brought forth, that *Stenodus* possesses many primitive features shared by both the Coregoninae and Salmoninae.

Comparison with Other Fossil Salmonids—There is practically no published fossil record for *Oncorhynchus* in North America. Jordan (1907) referred to a few toothed bones from Pleistocene Fossil Lake, Oregon, but these specimens are very doubtfully those of an *Oncorhynchus* (see Uyeno and Miller, 1963). An otolith of *O. tshawytscha* was recently reported and illustrated from Pleistocene sands in northern California (Fitch, 1970: 27). Although Neave (1958) expressed the view that *Oncorhynchus* arose from *Salmo* during Pleistocene time, evidence presented below shows that *Oncorhynchus* is at least as old as Middle Pliocene.

Fragmentary remains of what appears to be an extinct species of *Oncorhynchus* have been recovered from the Glenns Ferry Formation of southern Idaho. Identification is based on the anterior part of a dentary with three enlarged breeding teeth attached (Fig. 14 A) of the type characteristic of the spawning male *Oncorhynchus*. An incomplete left dentary and posterior half of a parasphenoid closely resemble those of *Oncorhynchus*. A median ridge located at the point of flection on the fossil parasphenoid (Fig. 14 B) matches that of *Oncorhynchus*, particularly *O. kisutch*.

Abundant remains of at least one extinct *Oncorhynchus*-like species have recently been found at the Worden Locality near Klamath Falls, southwestern Oregon (Fig. 14 E-I). They occur there in association with *Smilodonichthys*. The Worden specimens are distinguished from Recent species by the high coronoid re-

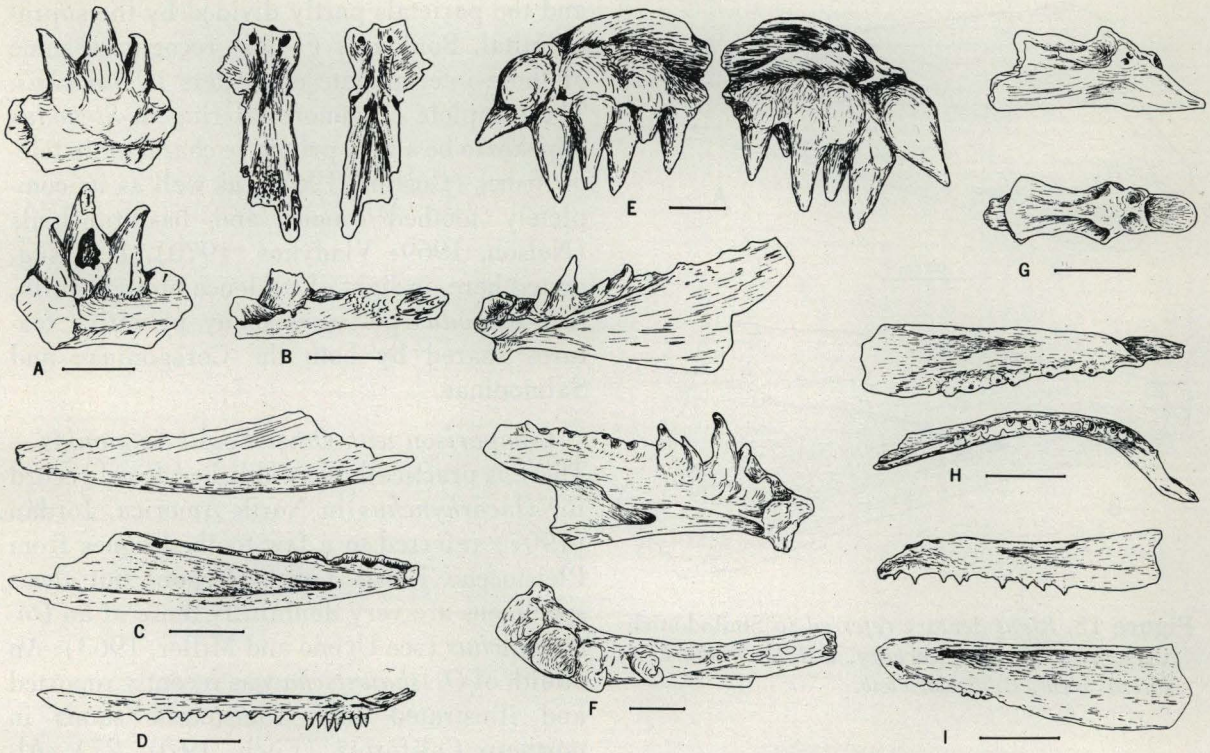

Figure 14. *A-C, specimens referable to* Oncorhynchus *sp. from the Glenns Ferry Formation, Idaho. A, anterior end of right dentary with breeding teeth attached, UMMP V58065, lateral view above, mesial below; B, posterior half of parasphenoid, UMMP V58066, ventral view above left, dorsal view above right, lateral view below; C, incomplete left dentary lacking teeth, UMMP V58067, lateral view above, ventral view below. D, complete right maxilla referable to* Oncorhynchus *sp. from the Fort Rock Formation, Oregon, UMMP V58068. E-I, specimens belonging to an undescribed* Oncorhynchus*-like salmonid from the Worden Locality, Oregon. E, complete left premaxilla with breeding teeth attached, UMMP V58069, lateral view to left, mesial view to right; F, incomplete left dentary with two breeding teeth attached, UMMP V58070, lateral view above, mesial view in middle, dorsal view below; G, posterior fragment of basioccipital showing occipital condyle, UMMP V58071, lateral view of left side above, dorsal view below; H, right maxilla with distal end missing, UMMP V58072, lateral view above, ventral view below; I, incomplete left maxilla in lateral view, UMMP V58073 (above), UMMP V58074 (below). Scale bars, 1 cm.*

gion of the mandible and by the form of the maxilla, both of which resemble *Smilodonichthys*. However, the jaw teeth of the Worden specimens are like those of *Oncorhynchus*. Of particular interest is the fragment of a parasphenoid showing a keel similar to that of *Smilodonichthys* but with an obliquely oriented condyle on the basioccipital (Fig. 14 G).

Another fossil salmonid pertinent to this discussion is *Rhabdofario*, described by Cope (1870) from Plio-Pleistocene deposits in southern Idaho. Uyeno and Miller (1963) subsequently synonymized *Rhabdofario* with *Salmo*. Cope distinguished his extinct fish from *Salmo* principally on the structure of the maxilla, in which it is markedly distinct from *Salmo*, but the form of this bone apparently does not separate *Rhabdofario* from *Oncorhynchus*. Re-examination of the holotype of *Rhabdofario* was necessary to determine its relationship (if any) to *Smilodonichthys* and *Oncorhynchus*. As pointed out previously, one of the most con-

sistent characters separating *Oncorhynchus* from *Salmo* is the azygous rostrum in the former which is reflected in the structure of the premaxilla. It is very difficult to determine which type of snout was present in *Rhabdofario* since the anterior portion of the right premaxilla is broken off in the holotype and the left bone is missing. Isolated premaxillae referable to *Rhabdofario* have been studied from the Cope collection and these show that the rostrum was forked as in *Salmo*.

Jaw and tooth structure of *Rhabdofario* indicates that it was a highly predaceous fish, most likely piscivorous in its feeding habits. Although the maxilla resembles that of *Oncorhynchus* and the premaxilla is like that of *Salmo*, other parts of the skull distinguish *Rhabdofario* from either genus. Because of the radically different feeding mechanism it represents a phyletic line well removed from *Smilodonichthys*.

UMMP collections also contain a right maxilla (Fig. 14 D) referable to *Oncorhynchus* that was found near Fossil Lake, Oregon, in diatomaceous (lacustrine) deposits of the Fort Rock Formation, which is of Middle to Upper Pliocene age (Hampton, 1964: B9). The proportions of the tooth-bearing shaft, shape and orientation of the anterior, articulating process, and the form of the teeth on this specimen all agree with *Oncorhynchus* rather than with *Salmo* or *Salvelinus*. In the straightness of the tooth-bearing edge, this maxilla is closest to that of Vladykov's (1962:170) species group (a), which consists of *Oncorhynchus gorbuscha*, *O. keta* and *O. nerka*.

SUMMARY

Smilodonichthys rastrosus n. g., n. sp., a giant salmon-like fish, is described from Pliocene stream deposits in California and Oregon. A combination of distinctive morphological features determined chiefly from a large, well-preserved skull, supports generic separation from *Oncorhynchus*, closest relative of the fossil. Specialized traits are the possession of over 100 long and toothless gill rakers, a keeled parasphenoid, an interopercle with a marked dorsal process, a toothless maxilla with enlarged supramaxilla, and a pair of huge premaxillary breeding teeth. A detailed account is given of the cranial osteology.

Comparison of osteological features of *Smilodonichthys* with those of the three salmonid subfamilies shows that the fossil possesses a number of primitive features. Postcranial parts are represented principally by disarticulated vertebral centra and nothing is known of the body and fin form in *Smilodonichthys*.

Relationship to *Oncorhynchus* is based on the form of the premaxilla, the type of breeding teeth, and the dermal bone structure.

The osteological features related to feeding are interpreted as being modified for capturing small organisms in a pelagic environment, probably the ocean. The premaxillary breeding teeth functioned in the reproductive display behavior. Their large size along with the internal organization of the dermal bone indicate that *Smilodonichthys* was anadromous.

Evaluation of recently collected salmonid fossils from western North America indicates that *Oncorhynchus* was present in the Pliocene, most likely contemporaneously with *Smilodonichthys*.

REFERENCES CITED

Allis, E. P., Jr., 1897, The cranial muscles and cranial and first spinal nerves in *Amia calva*: Jour. Morph., v. 12, pp. 487-808.

Bardack, D., 1965, Anatomy and evolution of chirocentrid fishes: Univ. Kan. Paleo. Contr., Vert., Art. 10, 88 pp.

Behnke, R. J., 1968, A new subgenus and species of trout, *Salmo* (*Platysalmo*) *platycephalus*, from Southcentral Turkey, with comments on the classification of the subfamily Salmoninae: Mitt. Hamburg. Zool. Mus. Inst., v. 66, pp. 1-15.

Berg, L. S., 1948, Freshwater fishes of the U.S.S.R. and adjacent countries: Akad. Nauk SSSR Zool. Inst., v. 1, pp. 1-504.

Boulenger, G. A., 1895, Remarks on some cranial characters of the salmonoids: Proc. Zool. Soc. London, v. 20, pp. 299-302.

Cavender, T., 1969, An Oligocene mudminnow (family Umbridae) from Oregon with remarks on relationships within the Esocoidei: Occ. Pap. Mus. Zool. Univ. Mich., 660, 33 pp.

————, 1970, A comparison of coregonines and other salmonids with the earliest known teleostean fishes. *In*: Biology of coregonid fishes, C. C. Lindsey and C. S. Woods, eds., pp. 1-32. Univ. Manitoba Press, Winnipeg.

Chapman, W. M., 1941, The osteology and relationships of the isospondylous fish Plecoglossus altivelis Temminck and Schlegel: Jour. Morph., v. 68, no. 3, pp. 425-455.

————, 1942, The osteology and relationships of the Argentinidae, a family of oceanic fishes: Jour. Wash. Acad. Sci., v. 32, no. 4, pp. 104-117.

Cope, E. D., 1870, On the fishes of a fresh-water Tertiary [lake] in Idaho, discovered by Capt. Clarence King: Proc. Amer. Philos. Soc., v. 11, pp. 538-547.

Evernden, J. F., D. E. Savage, G. H. Curtis, and G. T. James, 1964, Potassium-argon dates and the Cenozoic mammalian chronology of North America: Amer. Jour. Sci., v. 262, no. 2, pp. 145-198.

Fitch, J. E., 1970, Fish remains, mostly otoliths and teeth, from the Palos Verdes Sand (late Pleistocene) of California: Contrib. Sci. Los Angeles Co. Mus., no. 199, 41 pp.

Gardiner, B. G., 1967, The significance of the preoperculum in actinopterygian evolution: Jour. Linn. Soc. London (Zool.), v. 47, pp. 197-209.

Goody, P. C., 1969, The relationships of certain Upper Cretaceous teleosts with special reference to the myctophoids: Bull. Brit. Mus. (Nat. Hist.) Geol., supplement 7, 255 pp.

Gosline, W. A., 1961, Some osteological features of modern lower teleostean fishes: Smithsonian Misc. Coll., v. 142, no. 3, pp. 1-42.

————, 1965, Teleostean phylogeny: Copeia, 1965, no. 2, pp. 186-194.

————, 1969, The morphology and systematic position of the alepocephaloid fishes: Bull. Brit. Mus. (Nat. Hist.) Zool., v. 18, no. 6, pp. 185-218.

Greene, C. W. and C. H. Greene, 1914, The skeletal musculature of the king salmon: Bull. U.S. Bur. Fish., v. 33 (1913), pp. 21-60.

Greenwood, P. H., 1968, The osteology and relationships of the Denticipitidae, a family of clupeomorph fishes: Bull. Brit. Mus. (Nat. Hist.) Zool., v. 16, no. 6, pp. 213-273.

————, 1970, Skull and swimbladder connections in fishes of the family Megalopidae: Bull. Brit. Mus. (Nat. Hist.) Zool., v. 19, no. 3, pp. 121-135.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers, 1966, Phyletic studies of teleostean fishes, with a provisional classification of living forms: Bull. Amer. Mus. Nat. Hist., v. 131, art, 4, pp. 339-456.

Hampton, E. R., 1964, Geologic factors that control the occurrence and availability of ground water in the Fort Rock Basin, Lake County, Oregon: U.S.G.S. Prof. Pap. 383-B, pp. B1-B29.

Hikita, T., 1962, Ecological and morphological studies of the genus *Oncorhynchus* (Salmonidae) with particular consideration on phylogeny: Sci. Rept. Hokkaido Salmon Hatchery, no. 17, pp. 1-97.

Himberg, K-J. M., 1970, A systematic and zoogeographic study of some North European coregonids. *In*: Biology of coregonid fishes, C. C. Lindsey and C. S. Woods, eds., pp. 219-250. Univ. Manitoba Press, Winnipeg.

Jordan, D. S., 1907, The fossil fishes of California, with supplementary notes on other species of ex-

tinct fishes: Bull. Univ. Calif. Dept. Geol., v. 5, no. 7, pp. 95-144.

Kliewer, E. V., 1970, Gillraker variation and diet in lake whitefish *Coregonus clupeaformis* in northern Manitoba. *In*: Biology of coregonid fishes, C. C. Lindsey and C. S. Woods, eds., pp. 147-165. Univ. Manitoba Press, Winnipeg.

McAllister, D. E., 1968, Evolution of branchiostegals and classification of teleostome fishes: Bull. no. 221, Nat. Mus. Canada, 239 pp.

McDowall, R. M., 1969, Relationships of galaxioid fishes with a further discussion of salmoniform classification: Copeia, 1969, no. 4, pp. 796-824.

Morton, W. M., 1965, The taxonomic significance of the kype in American salmonids: Copeia, 1965, no. 1, pp. 14-19.

Neave, F., 1958, The origin and speciation of *Oncorhynchus*: Trans. Royal Soc. Canada, v. 52, ser. 3, sec. 5, pp. 25-39.

Nelson, G. J., 1969, Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates: Bull. Amer. Mus. Nat. Hist., v. 141, art. 4, pp. 475-552.

———, 1970, The hyobranchial apparatus of teleostean fishes of the families Engraulidae and Chirocentridae: Amer. Mus. Novitates, no. 2410, 30 pp.

Newcomb, R. C., 1958, Yonna formation of the Klamath River basin, Oregon: Northwest Sci., v. 32, no. 2, pp. 41-48.

Norden, C. R., 1961, Comparative osteology of representative salmonid fishes with particular reference to the grayling (*Thymallus arcticus*) and its phylogeny: Jour. Fish. Res. Bd. Canada, v. 18, no. 5, pp. 679-791.

———, 1970, Evolution and distribution of the genus *Prosopium*. *In*: Biology of coregonid fishes, C. C. Lindsey and C. S. Woods, eds., pp. 67-80. Univ. Manitoba Press, Winnipeg..

Nybelin, O., 1962, Preliminary note on two species previously named *Leptolepis bronni* Agassiz: Ark. Zool., v. 15, no. 2, pp. 303-306.

———, 1966, On Certain Triassic and Liassic representatives of the family Pholidophoridae s. str.: Bull. Brit. Mus. (Nat. Hist.) Geol., v. 11, pp. 351-432.

Patterson, C., 1967, Are the teleosts a polyphyletic group?: Colloques Internat. Centre Nat. Rech. Sci., vol. 163, pp. 93-109.

Rayner, D. H., 1948, The structure of certain Jurassic holostean fishes, with special reference to their neurocrania: Philos. Trans. Roy. Soc. London (ser. B), vol. 233, no. 601, pp. 287-345.

Ridewood, W. G., 1904, On the cranial osteology of the fishes of the families Elopidae and Albulidae, with remarks on the morphology of the skull in the lower teleostean fishes generally: Proc. Zool. Soc. London 1904, pt. 2, pp. 35-81.

———, 1905, On the cranial osteology of the clupeoid fishes: Proc. Zool. Soc. London, v. 2, pp. 448-493.

Rosen, D. E., and P. H. Greenwood, 1970, Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes: Amer. Mus. Novitates, no. 2428, 25 pp.

———, **and C. Patterson,** 1969. The structure and relationships of the paracanthopterygian fishes: Bull. Amer. Mus. Nat. Hist., v. 141, art. 3, pp. 357-374.

Rounsefell, G. A., 1962, Relationships among North American Salmonidae: Fish. Bull. U.S. Fish and Wildlife Serv., v. 62, pp. 235-270.

Shaposhnikova, G. Kh., 1968, A comparative morphological study of taimen (*Hucho* Günther) and lenok (*Brachymystax* Günther): Voprosy Ikhtiologii, v. 8, no. 3, pp. 351-370. (Translation).

Stirton, R. A., 1939, Cenozoic mammal remains from the San Francisco Bay region: Univ. Calif. Dept. Geol. Sci. Bull., v. 24, pp. 339-410 (see page 366 for localities 1037, V2572, and V3425, with faunal list).

Svetovidov, A. N., 1964, Systematics of the North American anadromous clupeoid fishes of the genera *Alosa*, *Caspialosa*, and *Pomolobus*: Copeia, 1964, no. 1, pp. 118-130.

Tchernavin, V. V., 1938, Changes in the salmon skull: Trans. Zool. Soc. London, v. 24, pt. 2, pp. 103-184.

———, 1943, The breeding characters of salmon in relation to their size: Proc. Zool. Soc. London, ser. B., v. 113, pp. 206-232.

———, 1953, The feeding mechanisms of a deep sea fish: Brit. Mus. (Nat. Hist.), Dept. Zool., 101 pp.

Tominaga, Y., 1966, On two tuna-like fishes captured in waters at about 40° S. lat.: Jap. Jour. Ichthyol., v. 14, pp. 41-48.

Uyeno, T., and R. R. Miller, 1963, Summary of late Cenozoic freshwater fish records for North America: Occ. Pap. Mus. Zool. Univ. Mich., no. 631, 34 pp.

Vladykov, V. D., 1962, Osteological studies on Pacific salmon of the genus *Oncorhynchus*: Bull. no. 136, Fish. Res. Bd. Canada, 172 pp.

————, 1970, Pearl tubercles and certain cranial peculiarities useful in the taxonomy of coregonid genera. *In*: Biology of coregonid fishes, C. C. Lindsey and C. S. Woods, eds., pp. 167-193. Univ. Manitoba Press, Winnipeg.

Weitzman, S. H., 1967, The origin of the stomiatoid fishes with comments on the classification of salmoniform fishes: Copeia, 1967, no. 3, pp. 507-540.

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